The Effect of a Storm on an Inshore Area with Markedly Stratified Waters

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ABSTRACT

Coincident with the formation and subsequent movement of a North Atlantic cyclone following the characteristic track, offshore surface waters are forced to the south coast of Nova Scotia with consequent removal of intermediate and bottom waters. Wind action, as the storm approaches, intensifies the mixing of the waters. Markedly stratified waters are thus temporarily replaced by a body of thoroughly mixed water.

INTRODUCTION

The purpose of this paper is to demonstrate, from observed conditions, the effect of a storm on an inshore area of markedly stratified waters. The hydrographical conditions in the water area off the south coast of Nova Scotia were investigated at a time during which a North Atlantic tropical cyclone was forming and subsequently moving along the characteristic track of these cyclones (Hachey 1934).

In certain cases it is important to distinguish between: (a) the effect on the water area of a steep pressure-gradient in the atmosphere above, a condition which is sufficient to set up gradients in the water area with resultant movements. Such movements, observed in the vicinity of the coast, may give ample warning of an approaching storm; and (b) the propulsive effect of the wind (which accompanies the storm) over the water area. In this paper, however, such distinctions have no special significance, for the action of the storm is measured solely by the observed conditions.

AN AREA OF MARKEDLY STRATIFIED WATERS

The water area off the south coast of Nova Scotia may be considered as an area of markedly stratified waters. Figure 1 illustrates, in section, the distribution of temperature and salinity as determined from observations during the period Aug. 19 to Aug. 22 inclusive, during the summer of 1932. The data for this period are given in table I. Three distinct layers of water are of importance in the area as follows: (a) the upper layer, consisting of water of a salinity less than 32.00‰ (as low as 30.65‰), and a temperature greater than 5.0°C. (as high as 19.3°C.); (b) the intermediate layer, consisting of water of a salinity

between 32.00‰ and 33.50‰, and a temperature less than 5.0°C. (as low as 1.1°C.); and (c) the bottom layer, consisting of water of a salinity greater than 33.50‰ (as high as 34.74‰), and a temperature greater than 5.0°C. (as high as 7.7°C.).

The hydrographical conditions in this area were investigated at monthly intervals throughout the summer of 1932. The main features changed but little. The upper layer gradually thickened as summer progressed, with increasing surface temperatures and a slight general lowering of salinities. The intermediate

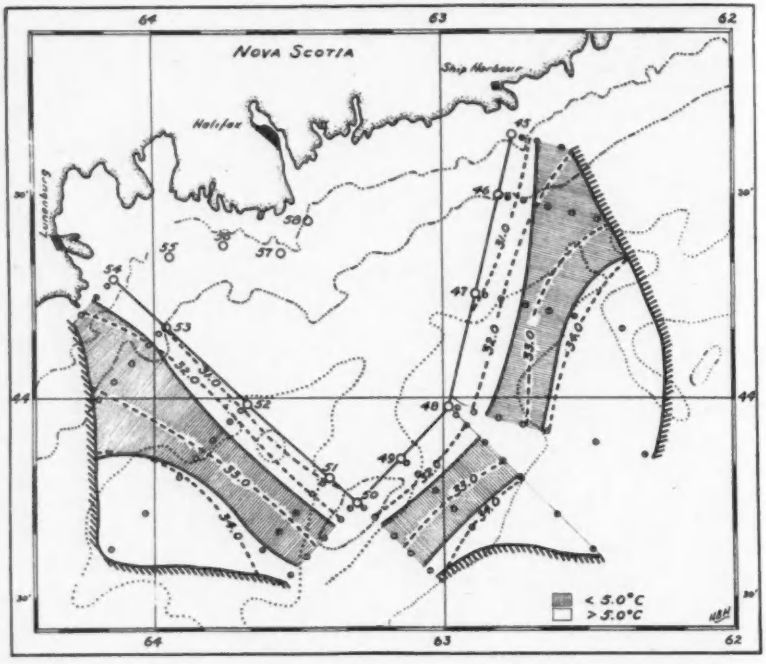

FIGURE 1. Distribution of temperature and salinities in section for August, 1932.

layer became slightly warmer, with the minimum temperature increasing from −0.4°C. in June to 1.8°C. in early October.

In figure 2, the dynamic gradients [as determined according to the method of Smith (1925), with modifications for inshore waters as suggested by Jacobsen and Jensen (1926)] are used to illustrate the surface movements of the waters of the area. The greatest resultant movement, as determined by this method, amounts to approximately 0.4 nautical miles (0.74 km.) per day (south-westerly along the coast and at right angles to a line joining stations 53 and 54). Throughout the summer this figure is fairly representative of the maximum resultant surface movement.

TABLE I. Observations of salinity and temperature for August, 1932. Gradient expressed in dynamic centimetres.

Depth (m.)	Salinity (‰)	Temperature (°C.)	Gradient
Sta. 45, 6.40-6.56 a.m., Aug. 19			
0	30.84	18.3	5.0
10	30.65	16.26	
25	31.34	4.66	4.6
50	31.81	2.20	4.6
Sta. 46, 8.33-9.01 a.m., Aug. 19			
0	30.84	18.3	4.8
10	30.74	16.87	
25	31.48	6.88	4.2
50	32.47	2.59	3.4
75	32.64	1.16	2.9
100	32.71	1.14	1.9
Sta. 47, 12.39-1.25 p.m., Aug. 19			
0	31.06	18.9	1.5
10	30.99	18.80	
25	31.94	9.30	0.9
50	32.68	2.21	0.4
75	33.42	3.66	0.6
100	33.86	5.34	0.6
150	34.55	7.62	0.5
175	34.70	7.88	
Sta. 48, 4.49-5.33 p.m., Aug. 19			
0	31.13	19.0	2.4
10	31.10	18.85	
25	32.11	10.36	1.8
50	32.53	1.61	1.1
75	32.84	2.52	0.8
100	33.96	5.80	0.4
150	34.58	7.57	0.4
200	34.74	7.68	2.2
Sta. 49, 2.19-2.47 p.m., Aug. 20			
0	31.06	19.3	2.2
10	31.01	19.01	
25	31.71	10.87	1.0
50	32.73	2.52	0.0
75	33.30	3.49	0.1
100	34.08	6.03	0.1
Sta. 50, 6.10-6.36 p.m., Aug. 20			
0	31.06	19.2	0.2
10	31.04	19.06	
25	32.07	6.27	0.2
50	32.64	2.43	0.3
75	.....	3.86	
100	33.94	5.79	0.7
Sta. 51, 7.37-8.09 p.m., Aug. 20			
0	31.06	19.2	0.4
10	30.99	18.96	
25	32.01	7.33	0.2
50	32.61	1.62	0.1
75	33.32	3.59	0.2
100	33.83	5.43	0.1
110	33.99	5.99	
Sta. 52, 10.05-10.53 a.m., Aug. 22			
0	30.93	19.3	0.1
10	30.92	18.23	
25	32.13	6.80	0.0
50	32.59	1.70	0.1
75	32.20	3.19	0.1
100	34.01	5.91	0.0
150	34.51	7.38	0.0
175	34.58	7.43	
Sta. 53, 2.03-2.26 p.m., Aug. 22			
0	30.86	18.1	1.6
10	31.53	11.92	
25	31.96	2.31	2.1
50	32.35	1.33	2.3
75	32.71	1.64	1.8
100	33.09	2.50	0.9
Sta. 54, 4.30-4.43 p.m., Aug. 22			
0	30.95	18.3	4.7
10	31.06	12.80	
25	31.27	5.96	4.3
50	32.03	1.90	3.0
Sta. 70, 6.06-6.27 a.m., Aug. 20			
0	31.11	19.0	0.0
10	31.06	17.42	
25	32.24	3.39	0.6
50	32.52	1.55	1.1
70	33.21	3.24	
Sta. 71, 8.40-9.24 a.m., Aug. 20			
0	31.01	19.0	1.1
10	31.04	18.91	
25	32.24	9.96	0.7
50	32.79	2.65	0.1
75	33.34	2.63	0.7
100	33.60	3.71	0.7
150	34.25	6.26	0.4
175	34.43	7.02	

TABLE I.—*Continued.*

Depth (m.)	Salinity (‰)	Temperature (°C.)	Gradient	Depth (m.)	Salinity (‰)	Temperature (°C.)	Gradient
Sta. 72, 11.37 a.m.-12.23 p.m., Aug. 20				Sta. 72 (cont'd)			
0	31.06	19.6	0.1	75	33.35	4.07	0.0
10	31.06	18.84		100	34.08	6.06	0.0
25	32.07	6.39	0.0	150	34.60	7.62	0.2
50	32.55	1.57	0.0	200	34.74	7.42	0.0

THE INSHORE AREA AND THE EFFECT OF A STORM

The immediate inshore area was investigated weekly throughout the summer by means of a series of stations extending from Halifax harbour outwards to a distance of about thirty miles (56 km.). Major changes in the nature and distribution of the waters in this coastal area are reflected to some extent in the waters of Halifax harbour. Weekly observations in the harbour throughout the year indicate that the major disturbances are coincident with storms of the north Atlantic ocean (Hachey 1934). In figures 3(a) and 3(b), the temperature and salinity observations made on Sept. 6 (data in table II) are plotted in section. It will be noted that the typical waters of the upper, intermediate, and bottom layers reach to this section. The conditions, as pictured here for Sept. 6, are typical of those throughout the summer period. The period was marked by quiet weather.

The month of September began with variable light winds which persisted until the 8th of the month. The wind, which on the 7th had been light WSW., shifted to light NE. and then to light ENE. on the 8th. On the 9th, the wind increased to strong NNE., continued on the 10th to strong NE. and N., and on the 11th to strong N. and fresh NNW. Thus there was a three-day period, following Sept. 8, when strong winds prevailed from a northerly direction. Rain fell on the 6th, 7th, 8th, 9th, and 10th of September.

The effect of this storm [a North Atlantic tropical cyclone following the characteristic track, Hachey (1934)] on the hydrographical conditions in the weekly section is shown in figures 3(c) and 3(d), where the temperature and salinity observations for Sept. 13 (data in table II) are plotted. The warm surface waters have been forced to the coast (although wind action would tend to offset this shoreward movement), producing a warm uniform body of water (temperatures ranging between 14.1°C. and 15.7°C.) in the area between stations 61 and 62. In the previous week (see figure 3(a)), the temperatures ranged from 4.0°C. on the bottom to 20.1°C. on the surface. The coldest water of the intermediate layer (less than 2.0°C.) has been almost entirely removed from the section, while the amount of water of a temperature less than 5.0°C. has been considerably decreased. The upper fifty metres, in the area between stations 60 and 62, has become practically uniform in salinity (30.72‰ to 30.82‰). This range of salinity differs considerably from the range in the same area during the previous week (30.95‰ to 32.03‰). The heavy rains which accompanied the storm are probably responsible for considerable freshening of the mixed water.

The upper ten metres of the offshore waters (station 59) consists of water of an average salinity of roughly 31.13‰, and an average temperature of roughly 15.2°C. with resulting average density of roughly 23.01. This is superposed on water of a salinity of 30.82‰ and a temperature of 13.2°C. with resulting density of 23.18 (found at station 59 at a depth of 25 metres). This latter sub-surface layer by reason of its salinity and temperature is the mixed water produced in the area between stations 60 and 62. It is thus seen that the mixed water resulting from the storm is of greater density than the offshore surface layers. Conse-

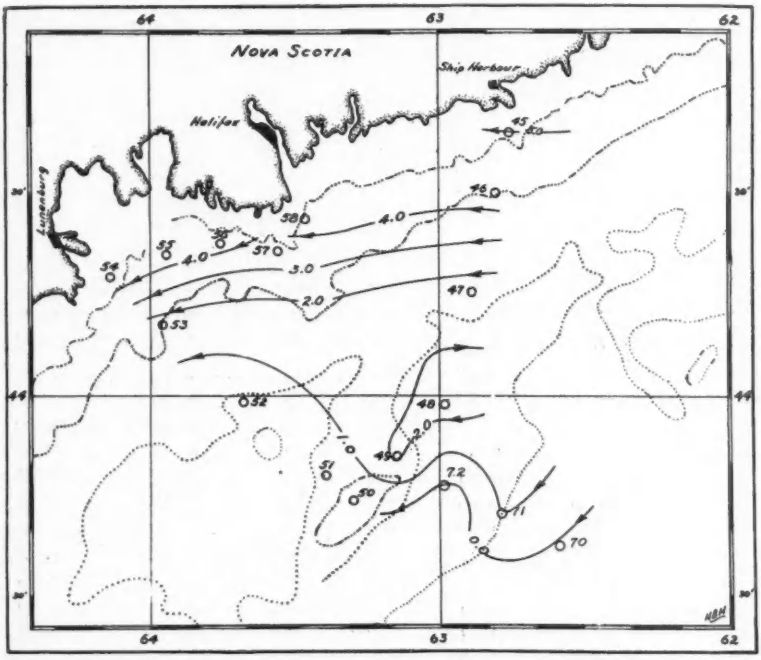

FIGURE 2. Surface water movements, August, 1932, as determined by the topography of the surface of the sea. Gradients expressed in dynamic centimetres.

quently, as the force of the storm is now spent, it must sink to some sub-surface level as it proceeds from the area of mixing.

On the whole, the picture of conditions as presented immediately following the storm is probably one of instability. By following the trend of conditions in the weeks following, such a supposition is verified. Other disturbances of less magnitude and shorter duration were noted from time to time, but the general trend after the storm subsided was towards the conditions found previous to the storm. Observations made on Oct. 10 (data in table II) are plotted in figures 3(e) and 3(f). The colder waters (less than 2.0°C.) form an integral part of the section, and stratification has become intensified throughout.

TABLE II. Observations of salinity and temperature (weekly section) for September 6, 12, and 13, and October 10 and 11, 1932.

Depth (m.)	Salinity (‰)	Temperature (°C.)
Sta. 59, 9.22-10.07 a.m., Sept. 6		
0	30.93	19.5
10	30.97	19.44
25	31.78	10.75
50	32.59	2.98
75	32.83	1.10
100	33.55	4.31
150	34.02	5.74
Sta. 60, 12.14-12.47 p.m., Sept. 6		
0	30.97	19.8
10	30.93	19.70
25	32.05	8.88
50	32.59	1.23
75	32.68	1.07
100	32.81	1.41
Sta. 61, 2.28-2.44 p.m., Sept. 6		
0	31.17	20.1
10	31.04	17.82
25	31.60	6.43
50	32.03	4.02
Sta. 62, 4.20-4.36 p.m., Sept. 6		
0	31.00	17.4
10	30.95	15.44
25	31.36	6.89
50	31.44	6.32
Sta. 531, 10.19-10.48 a.m., Sept. 6		
0	30.61	16.7
5	30.68	15.34
10	30.86	11.54
25	31.40	4.45
60	31.60	1.03
Sta. 533, 1.40-1.54 p.m., Sept. 6		
0	30.91	17.6
5	30.88	16.72
10	30.91	15.98
20	31.06	8.91
Sta. 59, 8.21-9.05 a.m., Sept. 13		
0	31.17	15.3
10	31.09	15.10
25	30.82	13.22
50	31.96	2.33
75	32.52	1.82
100	32.68	1.87
150	33.53	4.08

Depth (m.)	Salinity (‰)	Temperature (°C)
Sta. 60, 11.35 a.m.-12.08 p.m., Sept. 13		
0	30.53	16.0
10	30.53	14.64
25	30.82	13.46
50	30.82	12.06
75	31.51	6.52
100	31.82	4.98
Sta. 61, 1.53-2.08 p.m., Sept. 13		
0	30.61	15.7
10	30.55	15.35
25	30.57	15.34
50	30.62	14.88
Sta. 62, 3.44-3.58 p.m., Sept. 13		
0	30.75	15.5
10	30.72	15.30
25	30.86	15.15
30	30.91	14.14
Sta. 531, 10.19-10.48 a.m., Sept. 12		
0	30.61	16.7
5	30.68	15.34
10	30.86	11.54
25	31.40	4.45
60	31.60	1.03
Sta. 533, 1.35-1.52 p.m., Sept. 12		
0	30.52	14.7
5	30.53	14.24
10	30.55	13.94
20	30.93	9.34
Sta. 59, 10.14-10.52 a.m., Oct. 10		
0	30.86	13.3
10	30.73	12.66
25	30.82	12.57
50	32.14	5.39
75	32.48	2.03
100	32.88	1.94
150	34.02	5.76
Sta. 60, 12.28-12.58 p.m., Oct. 10		
0	30.82	13.8
10	30.77	13.01
25	31.24	11.28
50	31.98	6.30
75	32.47	2.33
100	32.74	1.56

TABLE II—*Continued.*

Depth (m.)	Salinity (‰)	Temperature (°C.)
Sta. 61, 2.20-2.34 p.m., Oct. 10		
0	31.17	13.8
10	31.24	12.01
25	31.62	9.43
50	32.23	4.52
Sta. 62, 4.04-4.16 p.m., Oct. 10		
0	30.81	13.0
10	31.56	9.64
25	31.78	7.72
30	31.87	7.00
Sta. 531, 10.04-10.35 a.m., Oct. 11		
0	29.79	14.4
5	29.96	13.85
10	30.84	11.04
25	31.44	6.76
60	31.55	1.18
Sta. 533, 1.30-1.41 p.m., Oct. 11		
0	30.08	14.2
5	30.16	13.20
10	31.24	10.09
20	31.73	8.49

GENERAL TREND OF BOTTOM CONDITIONS

In figures 4(a) and 4(b), the general trend of bottom conditions is shown for stations 533 and 61, the data being given in table III. Throughout the period (June to September) minor disturbances bring about small changes in temperature and salinity. The first indication of a disturbance of major importance is noted

TABLE III. Bottom salinities and temperatures for stations 533 and 61 for the summer period of 1932.

Station 533—Depth, 20 metres.				Station 61—Depth, 50 metres.			
Date 1932	Time	Salinity (‰)	Temp. (°C.)	Date 1932	Time	Salinity (‰)	Temp. (°C.)
June 4....	8.20 a.m.	31.42	4.16				
June 11....	8.25 a.m.	31.35	3.48				
June 17....	1.28 p.m.	31.36	2.33				
June 24....	12.26 p.m.	31.20	4.86	June 22....	2.38 p.m.	31.86	0.6
June 27....	1.33 p.m.	31.47	1.66	June 27....	1.08 p.m.	32.04	0.5
July 4....	1.00 p.m.	31.38	2.71	July 6....	1.50 p.m.	32.11	0.5
July 11....	1.57 p.m.	31.29	4.90	July 11....	11.23 a.m.	31.93	0.7
July 18....	1.04 p.m.	31.40	3.59	July 18....	12.50 p.m.	32.00	0.82
July 25....	1.40 p.m.	31.24	4.88	July 25....	1.16 p.m.	31.91	1.90
Aug. 1....	1.30 p.m.	31.35	5.36	Aug. 1....	2.15 p.m.	32.07	1.35
Aug. 8....	2.34 p.m.	31.26	6.34	Aug. 8....	12.59 p.m.	31.80	1.72
Aug. 15....	2.19 p.m.	31.44	5.21	Aug. 15....	5.13 p.m.	32.03	2.11
Aug. 22....	12.38 p.m.	31.13	7.29	Aug. 24....	4.55 p.m.	32.07	1.91
Aug. 29....	1.54 p.m.	31.53	5.06	Aug. 30....	12.48 p.m.	32.43	1.37
Sept. 6....	1.40 p.m.	31.06	8.91	Sept. 6....	2.28 p.m.	32.03	4.02
Sept. 12....	1.35 p.m.	30.93	9.34	Sept. 13....	1.53 p.m.	30.62	14.88
Sept. 19....	2.05 p.m.	30.64	14.19	Sept. 26....	2.01 p.m.	31.76	9.30
Sept. 26....	2.48 p.m.	30.91	12.58	Oct. 10....	2.20 p.m.	32.23	4.52
Oct. 6....	12.08 p.m.	31.46	9.03				
Oct. 11....	1.30 p.m.	31.73	8.49				

on Sept. 6, previous to the storm, when the salinity at station 533 decreased from 31.33‰ (Aug. 29) to 31.06‰ (Sept. 6), and the temperature increased from 5.06°C. to 8.91°C. A disturbance of similar magnitude is noted at station 61, where the salinity changed from 32.43‰ (Aug. 30) to 32.03‰ (Sept. 6), while the temperature changed from 1.37°C. to 4.02°C. At station 533, the salinity

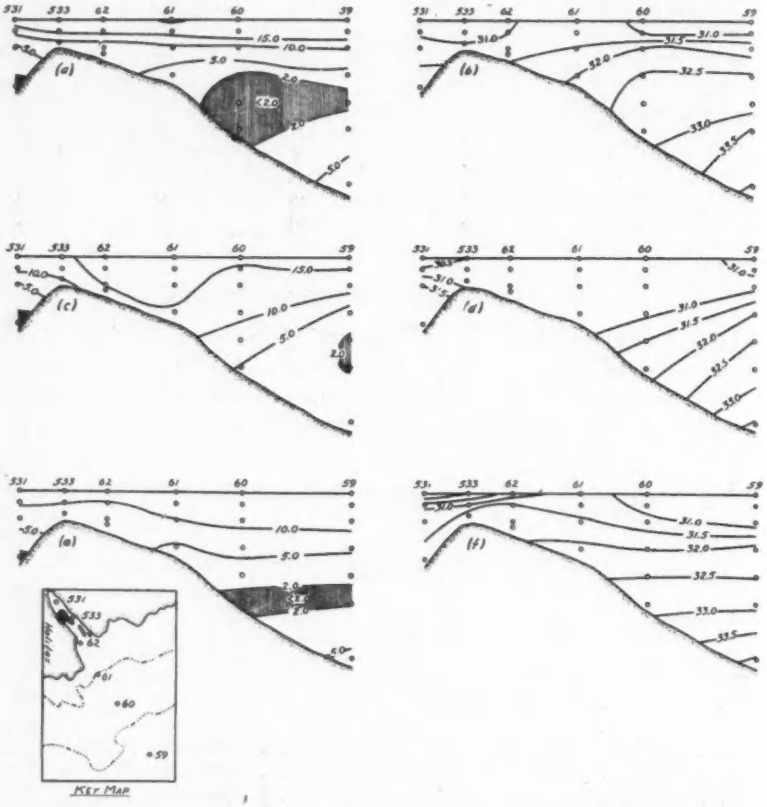

FIGURE 3. Distribution of temperatures and salinities in section. (a) temperature distribution, and (b) salinity distribution for Sept. 6, 1932; (c) temperature distribution, and (d) salinity distribution for Sept. 13, 1932; (e) temperature distribution, and (f) salinity distribution for Oct. 10, 1932.

and temperature were 30.93‰ and 9.34°C. respectively on Sept. 12, and 30.60‰ and 14.19°C. respectively on Sept. 19. At station 61, the salinity and temperature were 30.62‰ and 14.88°C. on Sept. 13.

During the period of extensive changes in the waters of the section (Aug. 30 to Sept. 19), steep pressure gradients existed over the ocean waters(McDonald 1932), with the pressure high over the Nova Scotia coast and low over the open ocean to the south. Such a distribution of pressure was probably responsible for

water movements which brought about sharp changes in temperatures and salinities and gave advance indications of the storm, which was finally experienced in the Halifax region from the 7th to the 11th of September. Wind action during this period was seemingly effective in bringing about thorough mixing of the waters. The full effect of the disturbance was operative at station 61 immediately, but did not operate fully at station 531 until at least a few days later. After the storm was spent (steep atmospheric pressure gradients no longer exist), both stations tended to get back to the original conditions. This was accomplished in a period of about six weeks.

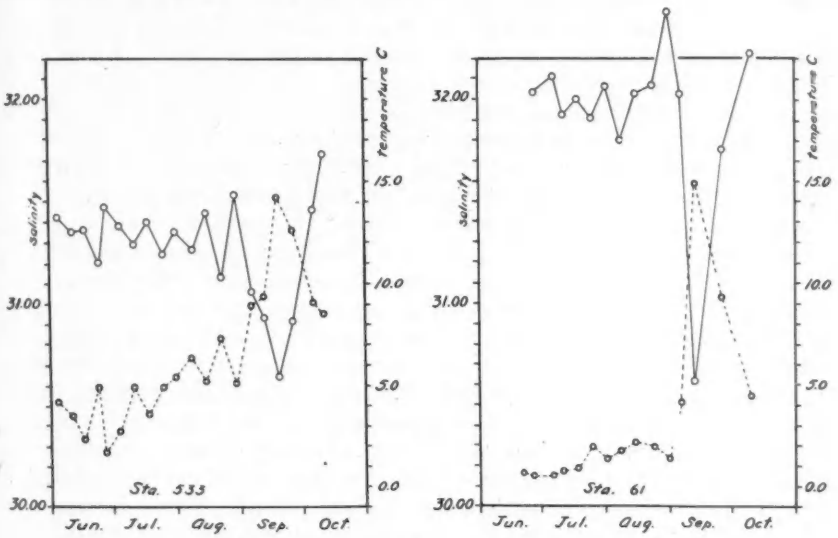

FIGURE 4. Variation in bottom temperatures and salinities at stations 533 and 61. 0————0, salinities; 0- - - - - - - - 0, temperatures.

DISCUSSION

The body of mixed water found at stations 61 and 62 after the storm is of a salinity of 30.61 ‰ to 30.91 ‰, and of a temperature of 15.7°C. to 14.14°C. Previous to the storm (Sept. 6), the temperature and salinity at stations 61 and 62 were as follows:

Depth (m.)	Station 61 Salinity ‰	Station 61 Temperature °C.	Station 62 Salinity ‰	Station 62 Temperature °C.
0	31.17	20.1	31.00	17.4
10	31.04	17.82	30.95	15.44
25	31.60	6.43	31.36	6.89
50	32.03	4.02	31.44	6.32

It is obvious that intense vertical mixing of these water columns will produce a water of a salinity greater than 31.00°/₀₀ and of a temperature less than 10.0°C. Consequently, as stations 61 and 62 are located in the area where intense mixing occurred, warmer waters must have been driven to the area and some freshening must have also taken place. Previous to the storm (Sept. 6), the upper ten metres of the section (stations 531 to 59) consisted of waters, of temperatures ranging from 11.54°C. to 20.1°C., and of salinities ranging from 30.61°/₀₀ to 31.17°/₀₀. Several days of rain accompanied the storm and this was probably responsible for the freshening that accompanied the mixing. Vertical mixing would tend to obviate the effects of the heavy rains, so it is probable that the mixed water is made up chiefly of the offshore waters of the upper ten metres, mixed inshore with water of the greater depths, and freshened by the heavy rains that accompanied the storm.

The density of the mixed water was roughly 23.18. This density is greater than the density of the surface waters further offshore (roughly 23.01 for the upper ten metres at station 59). Mixing involves the drawing of various waters to the mixing area and the distribution of the mixed water from the area. The mixed water, having in this case a density which is greater than that of the immediate offshore surface layer (the upper ten metres), must be distributed at some sub-surface level. Consequently, at station 59, we find some of this mixed water (salinity 30.82°/₀₀, and temperature 13.2°C.) at a depth of 25 metres, and covered by a layer of water of a mean salinity of approximately 31.13°/₀₀ and a mean temperature of approximately 15.2°C. As some of the mixed water (from the upper twenty-five metres at stations 61 and 62), sinks to a level of approximately 25 metres as it moves away from the mixing area, water must be drawn to the area in the upper twenty-five metres to replace it. In such a case, a movement of surface waters with a component towards the coast would result. Similarly, some of this mixed water (from depths greater than 25 metres) must be raised to approximately the 25-metre level as it moves away from the mixing area. A replacement of bottom waters must therefore occur. In this case, a movement of intermediate and bottom waters with components towards the coast must result. Such movements are probably responsible for the trend of conditions after the storm, for on Oct. 10 (see figures 3(e) and 3(f)) we find that waters from the surface layer, the intermediate layer, and the bottom layer again occupy the various portions of the section.

It has been shown previously (Hachey 1934) that the major disturbances in the region considered are due to storms. Steep atmospheric pressure gradients exist during these storms. Strong winds also prevail, but in the present case are such as tend to offset shoreward movement of the surface water. *Hence the probable and logical explanation would seem to be that the waters are reacting to the steep atmospheric pressure gradients.*

SUMMARY

1. The waters of the area are markedly stratified.

2. The months of June, July, and August, 1932, were marked by quiet weather. There was a three-day period following Sept. 8, when strong winds

prevailed from a northerly direction. Rain fell on the 6th, 7th, 8th, 9th and 10th of September.

3. A large body of mixed water was found in the inshore area after the storm.

4. The offshore surface waters were forced to the coast during the storm.

5. As the offshore waters were forced to the coast, the intermediate and bottom waters were forced to recede. As a result, bottom waters of comparatively low temperature and high salinity were replaced by waters, of offshore surface origin, of comparatively high temperature and low salinity.

6. Wind action intensified the mixing of the waters.

7. The mixed water, formed in the inshore area, was of greater density (roughly 23.18) than that of the offshore surface waters (roughly 23.01 for the upper ten metres at station 59). Consequently, when the storm subsided, this mixed water moved away from the area at depths determined by its density in relation to the density of the surrounding waters.

8. After the storm subsided, the general trend was towards conditions found previous to the storm.

9. Advance information of an approaching storm was given by the marked changes in bottom temperatures and salinities occurring at stations 533 and 61 between Aug. 29 and Sept. 6.

10. Steep pressure gradients in the atmosphere over the ocean, with the high pressure area in the vicinity of the coast and the low pressure area over the open ocean to the south, seemingly force waters of the surface layer towards the coast, and bring about removal of the deeper waters. Wind action, as the storm centre approaches, intensifies the mixing of the waters. With decreasing intensity, or reversed direction of the pressure gradients, the mixed water produced during the storm is forced offshore (moving at some subsurface level) and replaced through shoreward movements of the deeper waters.

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Vagal and Sympathetic Innervation of the Stomach in the Skate

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ABSTRACT

The distribution of autonomic nerves to the gastro-intestinal tract in *Raja diaphanes* and *R. stabuliforis* is described and figured. Stimulation of the vagus or of the anterior splanchnic nerve produces movements of the stomach, much stronger for the latter nerve. Stimulation of first one nerve, then the other, results in a summation of the two effects. Stimulation (if weak) of a branch of the vagus produces local contraction only. Atropine stimulates stomach movements without interfering with the effects of nerve stimulation. Small doses of adrenaline in lateral vein produce movements in same order as after stimulation of the sympathetic (anterior splanchnic).

ANATOMICAL RELATIONS

Although there are in existence several excellent accounts of the morphology of the autonomic nervous system in the *Selachii* (Chevrel 1887-90; Bottazzi 1902; Müller and Liljestrand 1918; Young 1933), none presents a view of the corresponding anatomical relations in a form which facilitates the task of the experimentalist. To meet this need we present below a brief description of the innervation of the gastro-intestinal tract, and the vascular supply thereto, of certain species of *Raja*, together with drawings made of actual dissections.

A gross-anatomical study was made of the distribution of the vagus and of the sympathetic nervous system to the gastro-intestinal tract. The blood vessels were injected with pyronine and Janus green and the course of the nervous branches was followed by means of a magnifying glass. *R. stabuliforis* (from 20 to 25 kg. in weight) and large specimens of *R. diaphanes* were used in this investigation.

Since the sympathetic nervous system follows the course of the arteries, a short description of the chief arteries in the abdominal cavity of the skate is here given. Daniel's (1928) terminology for the designation of the arteries has been used.

The coeliac axis at the level of the cardia gives off the gastro-hepatic branch and the anterior intestinal branch (A.I.A.). The gastro-hepatic artery is divided into the hepatic artery (H.A.), sending branches to the liver and gall-bladder, the anterior gastric artery (A.G.A.) and the ventral gastric artery (V.G.A.) (figures 1 and 2).

The anterior intestinal artery runs along the common bile duct to the duodenum. It gives off the following main branches: posterior gastro-splenic

artery (P.G.Sp.), intra-intestinal artery (I.I.A.), dorsal intestinal artery (D.A.) and pancreatico-splenic artery (P.S.A.) (figure 3).

The superior mesenteric artery (figures 2 and 4) supplies the dorsal part of the pyloric division of the stomach, the dorsal lobe of the pancreas and the spleen through the anterior gastro-splenic artery (A.G.Sp.—figure 4). Another branch of the superior mesenteric artery is the posterior intestinal artery (P.I.A.—figure 4). It runs along the dorsal wall of the intestine, almost up to the most posterior part, and gives off segmental annular branches.

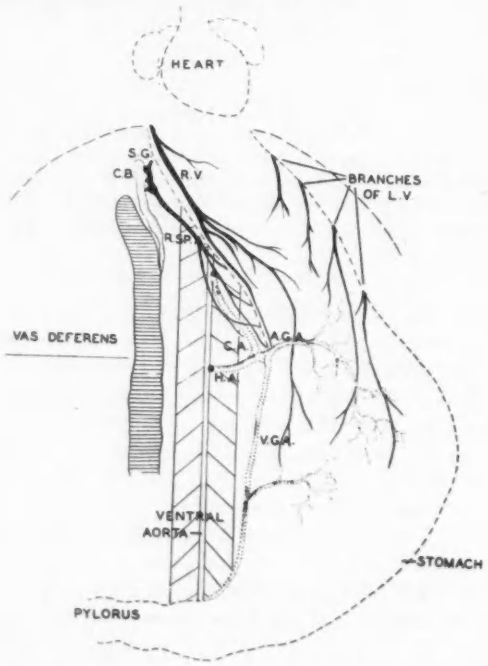

FIGURE 1. Semi-diagrammatic representation of distribution of the visceral branch of the vagus in the skate.

Explanation of lettering employed in this and other figures:

A.I.A., anterior intestinal artery; A.G.A., anterior gastric artery; A.G.Sp., anterior gastro-splenic artery; C.A. or C.A.A., coeliac axis; C.B., chromaffin body; C.B.D., common bile duct; D.A., dorsal intestinal artery; H.A., hepatic artery; I.I.A., intra-intestinal artery; L.I., large intestine; L.Sp.A., left anterior splanchnic nerve; L.V., left vagus nerve; P., pylorus; Pl., plexus; P.G.Sp., posterior gastro-splenic artery; P.I.A., posterior intestinal artery; P.S.A., pancreatico-splenic artery; R.Sp.A., right splanchnic nerve; R.V., right vagus; S., sinus; Sp.A., anterior splanchnic nerve; Sp.M., middle splanchnic nerve; S.G., sympathetic ganglion ("gastric ganglion"); $S.G._1$, first small sympathetic ganglion; $S.G._2$, second small sympathetic ganglion; $S.G._3$, third small sympathetic ganglion; S.M.A., superior mesenteric artery; V.G.A., ventral gastric artery.

Visceral Branch of the Vagus

Both intestinal branches of the vagus (figure 1) enter the abdominal cavity as two large nerve trunks. They lie under the tough membrane covering the oesophagus and both give off numerous branches to the oesophagus. Several branches also descend to the body of the stomach and about the middle of this

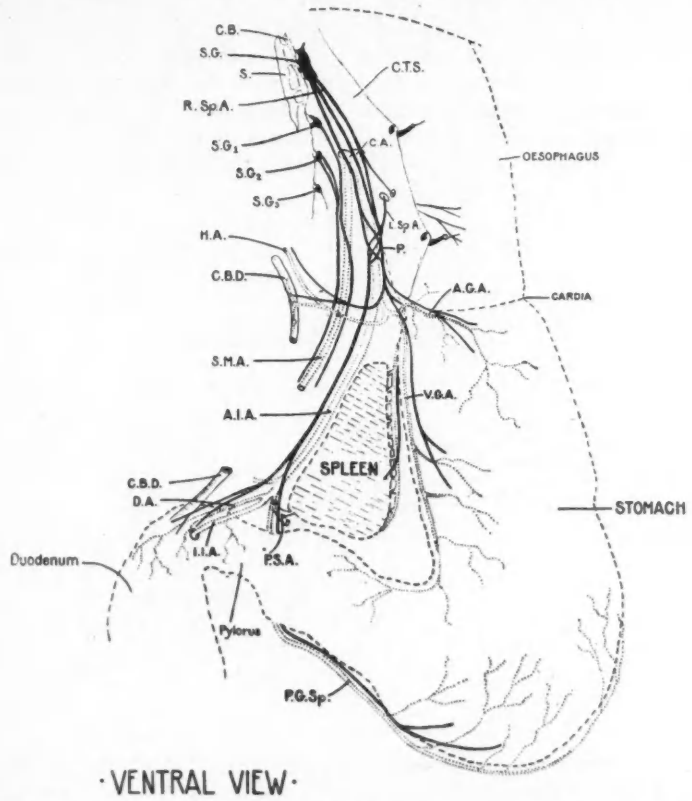

Figure 2. Semi-diagrammatic representation of the sympathetic nervous system on the right side in the skate.

organ disappear within the muscular tissue, so that they cannot be followed further with the naked eye. Müller and Liljestrand (1918) were able to trace the right vagus nerve to the anterior part of the cardiac division, where it divides into two branches. One of these follows the course of the gastric artery and one of the main branches of the anterior splanchnic nerves to the incisura angularis, where it breaks up into a number of small branches supplying the pyloric canal. The other branch of the vagus reaches the middle splanchnic nerves and supplies the intestine.

Sympathetic Innervation

On each side of the vertebral column may easily be seen a large and three or four comparatively smaller sympathetic ganglia, which send nerve branches to the gastro-intestinal tract chiefly along the arteries described above. Other sympathetic ganglia are found lying caudad, but these are much smaller than those belonging to the anterior group (figure 2—$S.G._1$, $S.G._2$ and $S.G._3$).

The first and largest sympathetic ganglion, the so-called gastric ganglion (S.G.), is connected closely with the anterior chromaffin body, forming the axillary body. The latter lies on the dorsal wall of the posterior cardinal sinus, where the smaller sympathetic ganglia are also found. The presence of inter-ganglionic fibres connecting the ganglia to form a chain is disputed. For a discussion of this problem reference may be made to the thorough anatomical study of Young (1933).

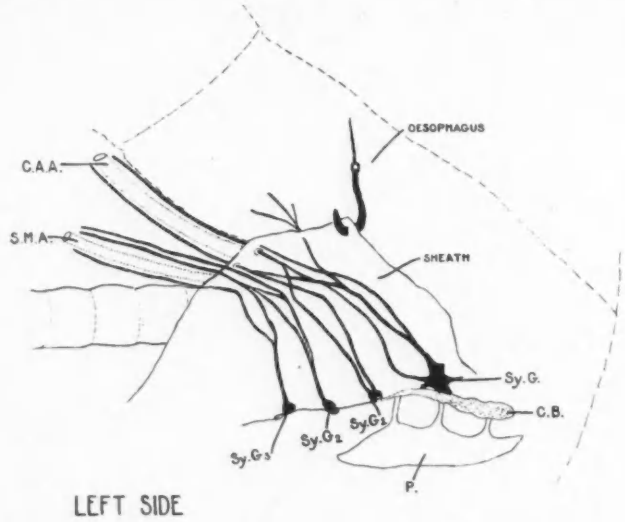

Figure 3. Semi-diagrammatic representation of the sympathetic nervous system on the left side in the skate.

Fine rami communicantes may easily be seen running from the spinal nerves to the gastric ganglion.

The large sympathetic ganglion on the right side (figure 2) usually gives off three nerve branches, which are called by Müller and Liljestrand (1918) anterior splanchnic nerves. These nerves pass caudalwards and join the coeliac axis. They run along the artery for a certain distance and are enclosed in the same sheath which surrounds the artery. In this region the nerves supply a few branches to the oesophagus and are connected by some fine fibres with the vagus nerve. At the level of the distal end of the oesophagus they join with the branches of the left anterior splanchnic nerves (figures 2 and 3) to form a plexus

(figure 2—Pl.) around the artery. From here on both sympathetic systems arising from the gastric sympathetic ganglia must be considered conjointly.

The left gastric sympathetic ganglion (figure 3) also usually gives off three nerve branches which join the coeliac axis and add to the formation of the plexus around it. On their course to the coeliac axis they also give off a few branches to the oesophagus.

At the level of the cardia the nerves surrounding the coeliac axis form three main divisions which follow the course of the three arteries, viz. the hepatic

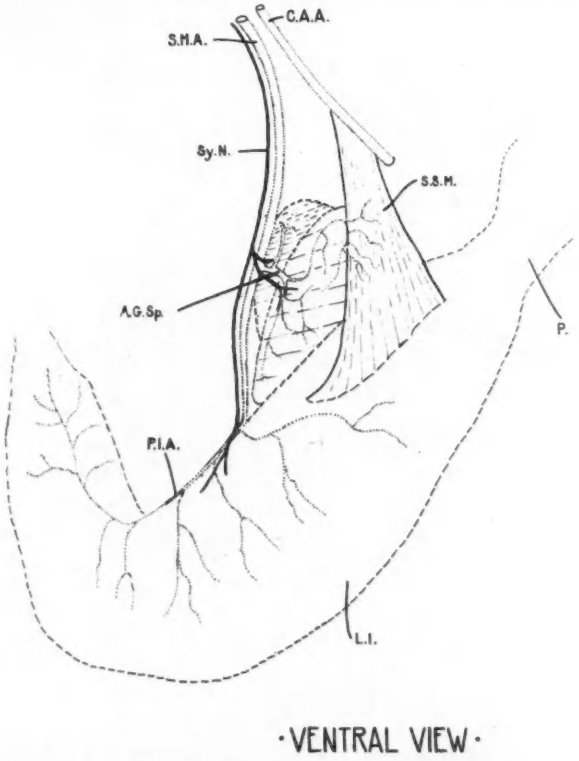

FIGURE 4. Semi-diagrammatic representation of the sympathetic nervous supply to the intestine in the skate.

(H.A.), the gastric (A.G.A. and V.G.A.) and the anterior intestinal (A.I.A.). Accordingly the sympathetic nerves supply the liver and the bile passages, the cardiac part of the stomach and a greater part of the lesser curvature, and also the spleen. The sympathetic nerve, following the anterior intestinal artery, divides at the pyloro-duodenal junction into two branches, one going to the duodenum, the other following the posterior gastro-splenic artery and supplying the pylorus and the greater curvature of the pyloric part of the stomach (figure

2). The two or three small sympathetic ganglia (figure 2—S.G.$_1$, S.G.$_2$ and S.G.$_3$) on the right side give off nerve branches to the superior mesenteric artery, the course and divisions of which they follow (figures 2 and 4). Müller and Liljestrand (1918) call these sympathetic fibres the "Nn. splanchnici medii". Before joining the superior mesenteric artery the nerve fibres from the corresponding ganglia on the left side form a kind of plexus on the oesophagus (figure 3). The sympathetic nerves following the course of the superior mesenteric artery supply the intestine, spleen and perhaps the pancreas.

Müller and Liljestrand (1918) describe a third set of fine nerve fibres in elasmobranchs, arising from the sympathetic ganglia which form the caudal end of the chain (Nn. splanchnici posteriores). They run partly free, and partly along the inferior mesenteric artery, to the caecum and rectum. It is very difficult to see them with the naked eye.

One of the many remarkable features of the sympathetic nervous system of elasmobranchs is that there are no large sympathetic ganglia on the way from the lateral sympathetic ganglia to the abdominal organs, such as exist in mammals. However, the great majority of the nerve fibres which leave the lateral sympathetic ganglia in elasmobranchs are non-medullated, post-ganglionic fibres. (Bottazzi 1902, Young 1933).

EXPERIMENTAL METHODS

For the study of stomach motility large specimens of *Raja diaphanes* and adult specimens of *Raja stabuliforis* were immobilized by section of the spinal cord below the medulla or by an intraperitoneal injection of Dial "Ciba" (0.3 to 0.4 cc. per kg.). Artificial respiration was applied by running sea-water through a cannula (or cannulae) inserted into one or both spiracles. In opening the abdomen care was taken to prevent the viscera coming in contact with the skin. Through small incisions in the stomach two balloons were introduced, one into the fundic, and the other into the pyloric portion of the stomach; these were connected to Marey's capsules and the contractions recorded on smoked paper. The recorded movements were controlled by direct observation of the movements of the viscera. A Harvard induction coil was used for nerve stimulation.

EXPERIMENTAL RESULTS

Vagus

Our method consisted of stimulating different branches of the vagus at the oesophagus. The upper branches of the vagus bear relations to the oesophagus only; stimulation with a faradic current produces an almost immediate contraction of the oesophagus. The other branches of the vagus have relation to both the oesophagus and the stomach. Stimulation of the vagus shows two remarkable features: (1) it produces an immediate contraction of the oesophagus and a contraction of the stomach which begins 25 to 45 seconds after the cessation of stimulation; (2) different branches of the vagus initiate contractions in different parts of the cardia and fundus, but if the current applied to a vagal branch is strong enough contractions spread all over the organ. The motor effect of vagus stimulation is shown in figures 6, 7 and 8.

A typical course of events when one of the vagal branches (in this case that on the right side of the oesophagus) was stimulated for 30 seconds with a moderately strong induction current (Harvard inductorium, coil 8 cm.) was as follows:

Experiment 2, Aug. 9. Raja stabuliforis.—Almost immediate contraction of the lower end of the oesophagus. Five to ten seconds after the beginning of stimulation, contraction of the pyloric sphincter occurred, lasting 5 to 10 seconds. Next there was a period with very few, if any, contractions, covering the rest of the stimulation period and the period immediately following cessation of stimulation. But 20 to 25 seconds after the end of the stimulation forward and backward movements of the lesser curvature and slight contractions of the pyloric canal began. A pulsating ring appeared in the cardiac part, and at times the body of the stomach would perform rotating movements.

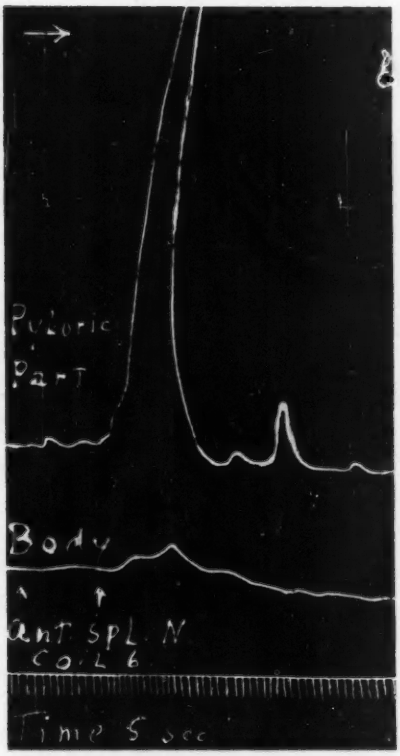

FIGURE 5. Exp. Aug. 15. *R. stabuliforis*, 27 kilos. One balloon introduced into the pyloric canal (upper curve), another into the body of the stomach (lower curve). Stimulation of anterior splanchnic nerves for 60 sec.

ANTERIOR SPLANCHNIC NERVES

The anterior splanchnic nerves, when stimulated, produce a much stronger and more prolonged effect than does the vagus. Almost immediately after stimulation a contraction of the lower end of the oesophagus would frequently appear. During the first 5 to 10 seconds the pyloric sphincter contracts. During

the remainder of the stimulation period (30 to 60 seconds) there are no movements whatsoever. The period of 25 to 30 seconds immediately following cessation of stimulation is also one of quiescence, after which a very strong contraction begins at the pyloric canal and spreads craniad. This contraction passes through the antrum pylori* and constricts the whole stomach; as the organ becomes narrower, it moves bodily caudad. The pyloric canal is constricted *in toto*, has a pencil-like appearance and is whitish in colour. Once or twice a contraction of the duodenum was noted, but this phenomenon was not so constant as the contraction of the stomach which could always be observed during and after stimulation of the nerves until they lost their excitability. About $1\frac{1}{2}$ minutes after the end of stimulation the whole stomach had constricted and then relaxed, these movements being repeated possibly several times (figure 5).

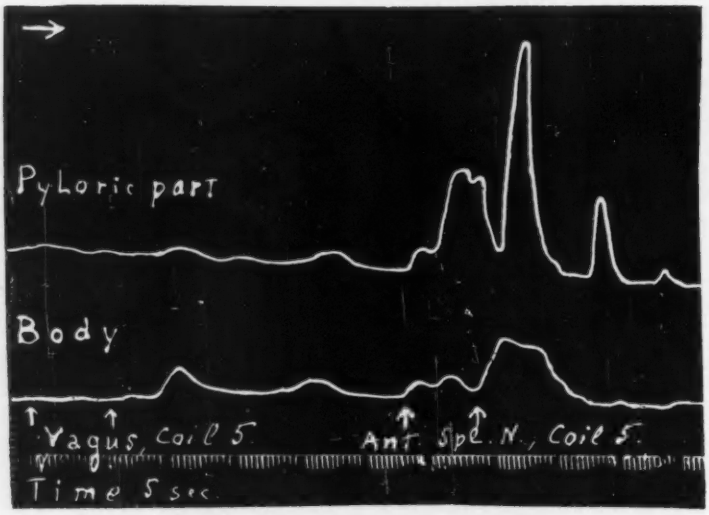

FIGURE 6. Exp. Aug. 15 (See figure 5). Summation of effect of stimulation of the vagus and anterior splanchnic nerves.

NN. SPLANCHNICI MEDII

Stimulation for 30 seconds (coil 5 cm.) gave the following results. During the stimulation only a slight contraction of the pylorus was noted. One to two minutes after the cessation of stimulation a strong ring of constriction appeared at the lower end of the large intestine and spread about one-third of the way up.

After several stimulations of the vagus and the anterior splanchnic nerve, in some experiments spontaneous contractions occurred in the form of travelling

*We propose tentatively to designate as "antrum pylori" the part lying between the corpus or body of the stomach and the pyloric canal in the skate. It is necessary to give a separate name (although perhaps a temporary one) to this region of the stomach on account of its special reaction to sympathomimetic drugs, described by Nicholls (1933).

rings. These started at the cardiac end of the stomach and descended to about the middle of the fundic part.

Müller and Liljestrand (1918) observed that vagus stimulation inhibited movements which had been provoked by splanchnic stimulation. In most of our experiments we found that stimulation of both nerves, either simultaneously or in rapid succession, produced no diminution in effect. In some cases, however, we observed that preliminary stimulation of the vagus actually increased the effect and shortened the latent period of splanchnic stimulation (see figure 6).

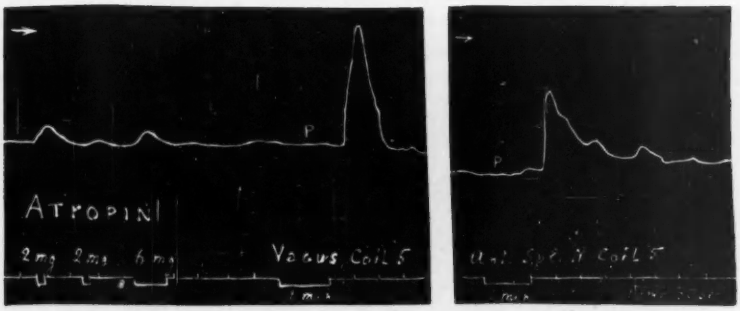

FIGURE 7. Exp. Aug. 23. *R. diaphanes*, 5½ kilos. Balloon inserted into the body of the stomach. Influence of atropine on the effect of vagus and anterior splanchnic nerve stimulation. Stimulation of the latter nerve applied almost immediately after stimulation of vagus. P., contraction of the pylorus and pyloric canal which was not recorded.

EFFECT OF ATROPINE

Atropine in large doses (6 to 10 mg.) did not prevent the positive effects of either vagus or splanchnic stimulation or of intravenous injection of adrenaline (figures 7 and 8). A small dose of adrenaline (2 cc. of 1:10,000 solution injected into the lateral vein of a skate of 5 kg.) produced quite distinct movements of the stomach in exactly the same order as stimulation of the anterior splanchnic nerves usually did (see figure 8). Atropine by itself stimulated movements of the stomach (figure 7) and in fact even increased the effect of vagus stimulation. Nicholls (1934) recently demonstrated that the effect of vagus stimulation on a strip of gastric muscle of skate is not affected by atropine, whereas the positive effect of acetylcholine is abolished by atropine.

DISCUSSION

The remarkable feature of the action of the parasympathetic and sympathetic nervous systems on the gastric motility in the skate is that both are of the excitatory type. This was shown by experiments in which both kinds of nerves were stimulated (Bottazzi 1902, Babkin and MacKay-Sawyer 1932, Lutz 1931) as well as by experiments in which parasympatho- and sympatho-mimetic drugs were employed (Dreyer 1928-29, Lutz 1931, Nicholls 1933, Young 1933). In the present investigation, not only was this observation confirmed, but it was also demonstrated that both nerves may act synergetically. That is, neither one in

any way hinders the positive effect of the other, and in certain cases one may even increase the positive effect of the other. Moreover, repeated stimulation of the vagus and the anterior splanchnic nerves sometimes induced automatic contractions of the stomach which were of peristaltic type. Müller and Liljestrand (1918) noted in some of their experiments that stimulation of the vagus superimposed on stimulation of the anterior splanchnic nerves inhibited the movements activated by the latter. As stated above, we did not observe any such inhibition. The possible explanation of Müller and Liljestrand's observation may be that usually the contractions appear after the cessation of stimulation of either of the nerves, and not during their stimulation. We cannot yet give any explanation of this peculiar relation of autonomic nerves to the tissue innervated

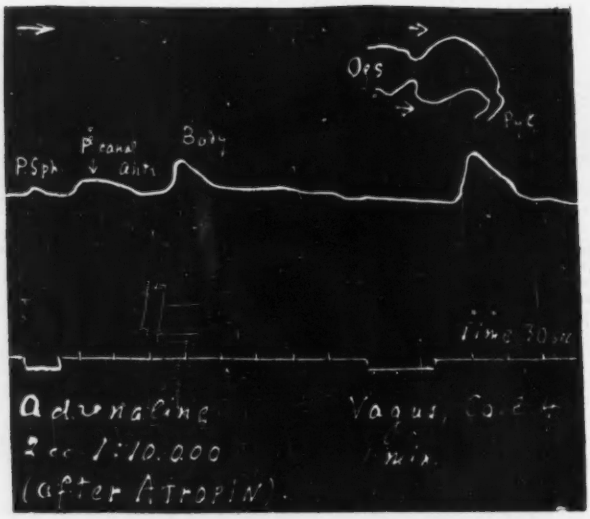

FIGURE 8. Exp. Aug. 23. Continuation of the experiment represented in figure 7. Previous injection of atropine did not hinder the stimulatory effect of adrenaline. Stimulation of vagus initiated a wave of contraction at the cardia, which did not travel very far.

by them in elasmobranchs. Müller and Liljestrand found that, if both nerves were stimulated simultaneously (the strength of the current employed is not stated by them), this period of inhibition could be very much emphasized. Undoubtedly more experiments are necessary to justify their claim that the vagus contains both motor and inhibitory fibres for the stomach. We therefore conclude that in elasmobranchs the relations between the two divisions of the autonomic nervous system, with regard to the activity of the muscle of the stomach, differ from those existing in mammals.

Nicholls (1933) showed that the spontaneous contractions of an isolated strip of antral muscle of the skate are inhibited by adrenaline in concentrations of 1:1,000,000 and greater, but that more dilute solutions (*e.g.*, 1:2,000,000)

cause stimulation. As mentioned above, we never observed any inhibitory effect of sympathetic (splanchnic nerve) stimulation on the motility of the stomach *in situ*. However, a careful study of the curves of contraction recorded by means of a balloon introduced into the distal part of the stomach (figure 8) shows that a wave of contraction spreading orally from the pyloric sphincter leaves the antrum unaffected. Nicholls (1934) also showed that the antral muscle of the skate's stomach, whose excitability had presumably been lowered through storage for 3 or 4 days in physiological media at 0° C., was stimulated by all effective doses of adrenaline. It may be supposed that the muscle of the antral region in the skate is more sensitive to adrenaline than are the muscles of other regions, and larger doses of this drug have an inhibitory action on it. The absence of marked relaxation of the antral region of the stomach in the intact animal during stimulation of the splanchnic nerves could be attributed on this ground to an insufficient liberation of "sympathin". It would seem that during the evolutionary history of the vertebrates the inhibitory properties of the sympathetic nervous system towards the muscles of the gastro-intestinal tract developed very gradually. Thus in amphibians (Dixon 1902, Langley and Orbeli 1910, Itagaki 1930) the sympathetic nerve to the stomach still retains the motor function. Young (1933), quite independently of us, also emphasizes the fact that there is very little evidence in elasmobranch fishes of a differentiation of the autonomic nervous system into the two antagonistic subdivisions found in mammals.

It is of great interest also to note that the smooth muscles of the arteries in the skate react to both adrenaline and acetylcholine by contraction (Babkin, Bowie and Nicholls 1933). Thus in animals so ancient from an evolutionary point of view as the elasmobranchs, differentiation of the muscular reaction towards parasympathetic and sympathetic "chemical transmitters" or "local hormones" has not yet appeared.

Another interesting feature of the effect of autonomic nerve stimulation on the stomach in the skate is that movements begin with contraction of the pyloric sphincter. These movements spread orally along the pyloric canal towards the body of the stomach and gradually involve the whole organ in a state of activity. It is therefore remarkable that the automatic movements of the stomach are always of a peristaltic and not of an antiperistaltic character. It is true that weak stimulation of separate branches of the vagus produces local contractions of the body of the stomach, but a stronger current as a rule initiates a general motor reaction. On stimulation of the anterior splanchnic nerves with an induction current of moderate strength, a general motor reaction of the whole stomach is the usual result.

These physiological findings may to a certain degree be explained by the histological structure of the "gastric plexus" described by E. Müller (1920). According to him the "gastric plexus" in selachians (*Squalus acanthias*) is a true nerve net in which the neurofibrils pass directly from one cell to another. He believes that within the plexus one may distinguish both vagal and sympathetic cells. The cells of the plexus are connected with the endings of nerve fibres which Müller believes are vagal in character. From his description one does not get a clear view of the relationship between the sympathetic fibres and

the gastric plexus. But if the extrinsic vagus and sympathetic nerve fibres are in some way connected with the nerve cells of the "gastric plexus", then the nerve impulses arriving at any point of this structure will activate movements in the whole organ.

SUMMARY

(1) The course and distribution of the vagus nerve and the anterior splanchnic nerve to the gastro-intestinal tract in *Raja diaphanes* and *Raja stabuliforis* are described.

(2) Both these nerves produce movements of the stomach in the skate. Neither of them inhibits these movements.

(3) Weak stimulation of various branches of the visceral vagus stimulates local contractions in different areas of the stomach. Stronger stimulation of the vagus sets up movements of the whole organ, beginning at the pylorus and proceeding craniad.

(4) Any effective stimulation of the anterior splanchnic nerve produces much stronger contractions than does vagus stimulation. The contraction always starts at the pylorus and moves towards the oesophagus.

(5) Stimulation of the vagus does not inhibit, but rather seems to facilitate the action of the sympathetic nerve.

(6) Atropine sulphate stimulates movements in the stomach and does not abolish the effect of vagus and sympathetic stimulation and of adrenaline.

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Factors Determining the Course of the Gastric Secretion in Elasmobranchs

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ABSTRACT

The continuous secretion of very small amounts of highly acid gastric juice in fasting skates (*Raja diaphanes* or *R. erinacea*) is unaffected by section of the vagi, injection of large doses of atropine, or subcutaneous introduction of histamine, but is inhibited for several hours by adrenaline or (to a less marked degree) by stimulation of the sympathetic.

Destruction of the spinal cord (cervical region to tail) results in a "paralytic" secretion of gastric juice (sympathetic influence eliminated), commencing after 1 day and continuing up to even 16 days, with volume up to 30 cc. per day, pH from 2.0 to 5.0, and digestive power moderate. The freezing point depression of the juice becomes progressively lower (Cl concentration unaltered), as also that of the blood. Secretion considered as very probably the result of vascular changes in the viscera due to disconnection of peripheral and central parts of the sympathetic.

INTRODUCTION

It is a well known fact that a skate or shark having food in its stomach when caught, or into whose stomach food is introduced, shows a strongly acid reaction in the stomach owing to the presence of gastric juice (Herwerden 1908, Herwerden and Ringer 1911). On the other hand, in fasting specimens it is hardly possible to aspirate any quantity of gastric juice although the reaction of the gastric mucosa is distinctly acid. There is therefore a causal relation between the ingestion of food and the secretion of gastric juice.

The stomach of the elasmobranchs possesses a well developed parasympathetic and sympathetic motor innervation (Babkin, Friedman and MacKay-Sawyer 1935). But the existence of a secretory innervation of the stomach in this species has been denied by Dobreff (1927), who came to this conclusion when he was unable to activate a gastric secretion by the use of sympatho- and parasympathomimetic drugs. Dobreff claimed that the mechanism of gastric secretion is purely humoral. A reinvestigation of the conditions regulating gastric secretion in elasmobranchs seemed to us the more desirable because Dobreff used only drugs in his attempts to stimulate a secretion.

METHODS

Several experimental methods were employed in our study of the gastric secretion in elasmobranchs. *Raja diaphanes* and *Raja erinacea* of various sizes

were used. In certain experiments intact animals were employed. The animal was taken from the water and a long narrow glass tube with rounded end was passed through the mouth into the stomach. By lifting the posterior part of the animal's body above the level of the tube and keeping the tube at a downward slant, any fluid which might be present in the stomach could be drained out. As a means of testing the reaction of the gastric mucosa (irrespective of that of the gastric juice), a long wire, to one end of which were attached red and blue litmus and congo red paper, was passed through the glass tube into the stomach.

In other experiments the spinal cord was destroyed by inserting a heavy wire probe through a cut in the ligament between the skull and the first vertebra and passing it down the spinal cord as far as the region of the vent. The site of insertion was then sutured. Animals with the cord so destroyed were kept alive for ten to sixteen days without feeding, during which time their gastric secretion was studied.

By the intra-abdominal injection of a very small dose of Dial "Ciba" (0.2 to 0.3 cc. or less per kilo weight) some sub-acute experiments were made possible. These operations consisted of tying a tube into the cardia, closing the oesophagus, tying the pylorus, etc. Animals with their abdomen opened for these purposes and closed again would survive for many hours or even days.

Acute experiments were resorted to in the endeavour to solve certain aspects of the problem. The spinal cord was cut below the medulla and artificial respiration was employed by inserting into one of the spiracles a glass tube through which sea-water was run. Further procedures in these experiments will perhaps be more clearly understood if considered in their proper places along with the results obtained.

Blood for the determination of chloride content and freezing point depression was obtained as described by Chaisson (1933); *i.e.*, a small glass cannula was ligated into the conus arteriosus and the blood was propelled into the test-tube by the force of the heart beat.

All pH determinations were made by means of capillator colorimeters (British Drug Houses). For the determination of pepsin, Mett's method, as modified by Nierenstein and Schiff (Hawk and Bergeim 1927), was used. Freezing point determinations were made in the usual manner by means of a Beckmann thermometer.

The only method available for chloride determination was that of Mohr and consequently the values obtained for blood plasma chlorides are only approximate.

RESULTS

Continuous Secretion of Gastric Juice

A fasting skate (unfed for 14 to 20 days) never has much fluid in its stomach. It is with great difficulty that even 0.5 cc. can be aspirated from such an animal. But the reaction of the gastric mucous membrane or of the small amount of fluid which may be aspirated is very acid to litmus and congo red.

Section of the vagi or injection of large doses of atropine did not abolish

this secretion; hence it does not depend on the integrity of the parasympathetic nervous system. Several experiments were performed which prove this point, of which the following are representative examples.

Exp. 34.—R. diaphanes, ♀ 1.475 kg. Aug. 17: 4.00 p.m., 0.5 cc. Dial given intra-abdominally. Stomach empty, reaction of mucosa very acid. 4.25 p.m., abdomen opened: oesophagus and pylorus tied with strong ligatures. Abdominal muscles and skin sutured separately. 4.35 p.m., operation ended. Aug. 18: 4.25 p.m., animal in good condition. Spinal cord cut below medulla, and abdomen immediately opened. Stomach contained about 2.0 cc. of acid mucoid fluid, pH 3.8. Reaction in fundus more acid than in pyloric canal.

In two other experiments (*exp. 26*, Aug. 13, and *exp. 27*, Aug. 14) a long glass tube was tied by strong ligatures into the lower end of the oesophagus, so that one end protruded a little from the mouth. The free end of the tube was corked so that sea-water could not enter the stomach. The abdominal wall was closed by stitches. The animals survived for 26 hours and 35 hours respectively. In both cases death was presumably due to compression of one of the abdominal venous sinuses owing to change in the position of the stomach end of the tube during the swimming movements of the animals. Nevertheless, in both cases the reaction of the stomach was definitely acid during the experiment and also immediately after death. The spontaneous secretions aspirated several times during the experiment were scanty. For example, in one of the animals the total secretion during 24 hours did not exceed 2.0 cc. of mucoid fluid, and in the other only 0.4 cc. (pH 3.3) was obtained 18 hours after tying of the vagi.

In another experiment (*exp. 24*, Aug. 11) the spinal cord was cut below the medulla and the whole brain then destroyed. Respiration ceased but the spinal reflexes still persisted. Two hours after the operation the spinal reflexes were found to be weaker but the reaction in the stomach was still strongly acid. Although the heart was still beating slowly 3 hours and 15 minutes after the operation, the spinal reflexes had gradually disappeared. The stomach contained about 12 cc. of sea-water and the reaction of the stomach had changed to neutral. Therefore the sea-water must have entered the stomach just before death, and probably as the result of paralysis of the muscles of the pharynx or of the cardia.

Five experiments were performed in which 2 to 5 mg. atropine sulphate were injected subcutaneously and intramuscularly. In all but one of the experiments the reaction in the stomach remained acid but no increase in secretion occurred in any of them. The following is quoted as an example.

Exp. 39.—*R. diaphanes*, ♂ medium size. Aug. 21: 2.20 p.m., stomach empty and acid. 4 mg. atropine sulphate injected subcutaneously and intramuscularly. Stomach empty for the next 5 hours, but reaction of the mucosa strongly acid. 7.35 p.m., 0.55 cc. thick mucus aspirated, with pH of 2.8 to 3.2. Aug. 22: 9.30 a.m., stomach empty and acid.

The exceptional case mentioned, in which the reaction did not remain acid, was as follows.

Exp. 20.—R. erinacea, ♀, about 1 kg. Aug. 8: 5 mg. atropine sulphate were injected at one time—3 mg. subcutaneously and, through error, 2 mg. intra-abdominally. For 4 hours the stomach was empty and its reaction acid. Then during the next 24 hours aspiration resulted each time in from 7 to 10 cc. of a neutral or slightly alkaline fluid, presumably sea-water. During the 24 hours following, the fluid became slightly acid again. The volume of fluid which could be aspirated gradually fell, and after 6 or 7 days the volume had again become small and the reaction acid. In this experiment the atropine probably disturbed the motor innervation of the pharynx or cardia, so that sea-water passed into the stomach.

It is important to note that in severe operations or shortly before death the acid secretion ceases and the reaction of the mucosa becomes neutral.

Exciting the animal does not in any way affect the spontaneous gastric secretion, nor does it make any difference whether it is kept for days in the shallow

laboratory aquarium, exposed to the full light of day, or in tanks in a dark cool cellar.

PARASYMPATHETIC INNERVATION

Several experiments were performed on spinal skates, in which a rubber balloon was introduced into the upper part of the oesophagus or else into the pharynx. The balloon was alternately distended and deflated repeatedly with air in order to produce a swallowing reflex and so to stimulate a gastric secretion through the vagi. To preserve the vagi intact, a longitudinal incision was made through the muscular layer of the oesophagus a little above the cardia. The submucous and mucous membranes were separated from the muscular layer with a blunt instrument. A glass tube, to which a rubber balloon was attached, was passed through the incision and into the upper part of the oesophagus, where it was tied to the submucous and mucous layers so as to leave the musculature free and the vagi intact. The oesophagus was thus separated completely from the stomach. A glass cannula was introduced into the pylorus and the pylorus was then tied at the duodenal junction. The animal was left lying supine on a board and respiration was applied in the usual manner by passing sea-water through one of the spiracles.

No definite results were obtained by stimulating the swallowing movements. For three or four hours the balloon was repeatedly distended and deflated. Each time the balloon was distended the animal performed swallowing movements, and the water which filled its buccal cavity was often expelled through the mouth. No secretion of gastric juice resulted and the reaction of the mucous membrane remained slightly acid or neutral.

Distension of the stomach in a spinal skate for several hours with an inflated balloon or with pieces of herring did not provoke a gastric secretion. This is in accordance with the fact that in mammals mechanical stimulation of the gastric mucosa is without effect on the secretion, but it is in strong contrast with the conditions found in the frog, in which mechanical stimulation results in a secretion (Friedman 1934).

No attempt was made to stimulate the visceral branches of the vagus because the operation required for this is difficult and might be too drastic for the animal; the results moreover would be doubtful owing to the possible inhibitory effect of the operation on gastric secretion.

The results of the experiments described above, when considered in conjunction with the negative results obtained by Dobreff (1927), make it seem very doubtful that the vagus nerve participates in gastric secretion. However, it is still possible that the vagus does convey some secretory impulses to the gastric mucosa in this species; if so, then special methods would be required for their study.

SYMPATHETIC INNERVATION

Several acute experiments, involving stimulation of the anterior splanchnic nerves, were performed, with Dial "Ciba" as an anaesthetic. The abdomen was opened, the oesophagus and pylorus tied, and a cannula fixed into the fundus. Although the nerves were stimulated at intervals over a period of 3½ to 4 hours,

and a typical motor reaction was always produced, yet no definite secretory effect was obtained. It is true that in some experiments the reaction of the gastric mucosa, which from acid had become neutral during the operation, again turned acid during the course of the experiment. However, this might have been due to the recovery of the animal from the operative shock, and not to the secretory effect of splanchnic stimulation. As it was possible that the inhibition of the secretion was the result of the operative procedure, we proceeded to carry out some experiments with adrenaline.

In acute experiments as well as in normal animals subcutaneous injection of adrenaline in various amounts (including massive doses) did not provoke a gastric secretion. Moreover, in many cases there was even an inhibition of the spontaneous secretion or of the secretion which had previously been produced by the presence of food in the stomach. The following examples illustrate this statement.

Exp. 47, Aug. 31.—*R. erinacea*, ♀ medium size. 8 cc. of adrenaline (1:5,000) were injected over a period of 8 hours. At the end of this peroid a little fluid and food, both having a neutral reaction, could be aspirated from the stomach. The reaction of the mucosa was also neutral.

Exps. 57 to 59, Sept. 5.—Three *R. erinacea*, medium size. These experiments were of more than 21 hours' duration. 2 cc. of adrenaline (1:10,000) were injected every 1½ hours, so that each animal received altogether 22 cc. of adrenaline. At the end of the experiments the findings were:

Exp. 57—stomach contained food; reaction acid.
" 58— " empty; reaction neutral.
" 59— " " " "

Therefore the conclusion may be drawn that the sympathetic nervous system does not convey secretory impulses to the gastric glands in the skate as it does in amphibia such as the frog, *Rana esculenta* (Friedman 1934). The inhibitory influence of splanchnic stimulation and of adrenaline on gastric secretion in the skate is probably due to vasoconstriction.

Effect of Histamine

This substance, known to be a very powerful stimulant of the gastric glands in warm-blooded animals, when introduced subcutaneously into the skate even in massive doses, neither augmented nor inhibited the spontaneous gastric secretion in normal animals. Thus in one experiment (*exp. 45*, Aug. 26) 2 mg. histamine monochloride were administered subcutaneously every two hours for a period of ten hours (total dose 10 mg.) without any effect.

In another series of experiments (*exps. 53 to 56*, Aug. 19) four skates were injected simultaneously with 2 mg. of histamine and 2 cc. of adrenaline (1:5,000). In three of the animals the initial acid reaction of the stomach became neutral in 12 hours.

In connection with the above it is interesting to note that MacKay (1931) found that histamine has no effect on the circulatory system of the skate.

Destruction of the Spinal Cord

As reported above, elimination of the vagus influence on the gastric mucosa did not produce any marked effect on the secretory function of the gastric glands.

Quite different results, however, were obtained when the sympathetic nervous system was eliminated by destruction of the spinal cord from the cervical region down to the tail. Destruction of the spinal cord results in a "paralytic" secretion of acid gastric juice. This comparatively voluminous acid secretion appeared in from about 24 hours to 3 or 4 days after the cord was destroyed, the time varying in the 10 experiments performed. The secretion continued to the end of the experiment, the longest duration of any of the experiments being 16 days, during which the animal did not of course receive any food. The amount of fluid which could be aspirated from the stomach varied widely in different animals, ranging from 1 cc. to 15 cc. per 24 hours, though the exact amount of juice secreted could not always be determined, since the integrity of the gastro-intestinal tract was preserved and part of the secretion probably passed into the intestine. Although sea-water may possibly have entered the stomach just after the operation, it is very improbable that it did so in the later stages of the experiment. It is possible that, immediately after the cord was destroyed, the oesophagus lost its tone or the tone of the sphincters was diminished so that water passed into the stomach. Sea-water, which has an average pH of 8.2, would be quite sufficient to neutralize the acid secretion. If poured on the acid mucosa of the stomach and kept there for one or two minutes, it turns the mucosa neutral or alkaline.

Two examples are quoted here of long-continued "paralytic" gastric secretion in skates with spinal cord destroyed, *exps. 18 and 51* (table I). The first animal was sacrificed 9 days, the second 16 days after the destruction of the cord.

TABLE I. "Paralytic" secretion of gastric juice in the skate after destruction of the spinal cord

Exp. 18.—R. erinacea, Aug. 7, stomach empty, reaction of gastric mucosa very acid. Spinal cord destroyed at noon. Killed Aug. 16.

Date	Vol. cc.	pH	Δ° C.
Aug. 8	no fluid	acid	
" 9	13.0	3.0	
" 10	7.0	3.2	
" 11	2.0	3.0	
" 12	1.8	2.8	
" 13	9.2	2.8	
" 14	9.5	2.8	1.662
" 15	10.0	3.0	1.667
	5.0	3.4	1.325
Aug. 16			
Juice	5.0	4.9	1.245
Blood			1.515
Sea-water			1.686

Exp. 51.—R. erinacea, Aug. 31, stomach empty, reaction of gastric mucosa very acid. Spinal cord destroyed at noon. Killed Sept. 15.

Date	Vol. cc.	pH	Cl gm. %
Sept. 1	5.0	6.2	1.780
" 2	1.2	3.2	1.801
" 4	1.0	3.0	1.854
" 5	2.0	2.5	1.818
" 6	3.0	2.5	1.813
" 7	0.5	2.5	.....
" 8	2.0	2.0	1.760
" 9	1.0	2.0	1.960(?)
" 11	0.5	2.0	.....
" 12	4.5	2.1	1.670
" 14	5.0	2.0	1.760
Sept. 15			
Juice	5.0	2.0	1.760
Blood plasma			0.929
Sea-water			1.804

N.B.—Average Δ of the local sea-water during summer = 1.72° C.

The freezing point depression of the acid gastric juice in the first skate (*exp. 18*) gradually diminished until it reached an extremely low value, $\Delta = 1.245°$ C. It was lower than the freezing point of the blood ($\Delta = 1.515°$ C.) and of the sea-water (average $\Delta = 1.72°$ C.). It is a remarkable fact that the Δ of the blood in this animal was much lower than the freezing point of the sea-water.

These findings on the blood of the skate are in accordance with the results previously obtained by one of us (Chaisson 1933), in which destruction of the spinal cord resulted in a lowering of the osmotic pressure of the blood (also Chaisson and Friedman 1935).

In the second animal (*exp. 51*) the chloride concentration of the acid gastric secretion varied from day to day, reaching on several occasions a concentration higher than that of the local sea-water (St. Andrews, N.B.). On Sept. 15, when the animal was killed, the Cl concentration of the juice was equal to 1.76 mg. per cent, whilst that of the sea-water was 1.804 mg. per cent. The blood plasma of this skate contained somewhat more Cl (0.929 gm. per cent) than is found in the normal animal (about 0.905 gm. per cent).

Injection of adrenaline stopped the acid "paralytic" secretion. In several experiments the stomach contained a neutral or slightly alkaline fluid; this was presumably sea-water because its Cl concentration and Δ were approximately those of sea-water. Experiment 33 may be cited as representative of several such experiments.

Exp. 33.—R. diaphanes, 1.25 kg. Had been kept in the laboratory for 19 days without food. Aug. 18: Stomach acid, no fluid. Spinal cord destroyed. Aug. 22: Stomach empty and acid. 10 a.m, 2 cc. adrenaline (1:10,000) injected subcutaneously and intramuscularly. 11.05 a.m., 0.5 cc. fluid aspirated from stomach, pH 7.2. 12.05 p.m., 23.0 cc. fluid, pH 7.6. 2.05 p.m., 4.5 cc. fluid, pH 7.6. The Cl of these fluids was 1.79 gm. per cent. (Another indication that the fluid was sea-water is that it could be aspirated from the stomach as soon as the animal was replaced in the aquarium tank but not when it was kept on a board.) Aug. 23: 8.15 a.m., 3.0 cc. acid fluid aspirated, pH 3.1, Cl 1.98 gm. per cent. The Cl concentration of the sea-water at this time was 1.80 mg. per cent. Aug. 24: 8.15 a.m., 3.6 cc. fluid, pH 3.7.

The evidence in favour of the theory that an actual secretion of gastric juice results from destruction of the spinal cord is as follows.

(1) The reaction of the gastric contents was acid, attaining sometimes a pH as high as 2.0.

(2) The osmotic pressure of the gastric contents was lower than that of the sea-water.

(3) The Cl concentration of the gastric contents did not always correspond to that of the sea-water but was sometimes lower and at other times higher.

(4) The secretion possessed a moderate peptic power, varying from 40 to 150 Mett's units (Nierenstein and Schiff's modification of Mett's method, as described by Hawk and Bergeim 1927).

(5) During the secretion of the "paralytic" juice both the secretion and the blood itself became gradually depleted of some substance, as may be judged from the gradual rising of the freezing point.

Control experiments, in which the spinal cord was not destroyed but was cut below the medulla, showed that this procedure does not produce a "para-

lytic" secretion. Only a few cc. of gastric juice could be aspirated occasionally. Thus:

Exp. 31.—R. diaphanes, 1.50 kg. Aug. 16: Stomach empty and reaction acid. Spinal cord cut below medulla. Stomach empty but strongly acid, until Aug. 19. Aug. 19: 3 p.m., 3.1 cc. of fluid, pH 3.8, were aspirated. During the following two days the stomach remained empty but its mucous membrane was strongly acid in reaction. Aug. 21: Animal killed. Blood $\Delta = 1.725°$ C.; sea-water $\Delta = 1.737°$ C.

Therefore the essential condition for the production of a "paralytic" gastric secretion seems to be the disconnection of the peripheral parts of the sympathetic nervous system from its central stations in the spinal cord. The greater part of the cord must be completely destroyed. When on some occasions a probe of insufficient thickness was used for the purpose of destroying the cord, presumably some points of the cord remained intact, since the animal, when touched, moved its pectoral fins and tail slightly. In such cases an acid gastric secretion did not appear, but instead the stomach was filled with a large amount of neutral fluid, presumably sea-water, just as in the first few hours after complete destruction of the spinal cord or after injection of adrenaline.

CONCLUSION

The object of this investigation has been to elucidate the mechanism of gastric secretion in elasmobranchs, a subject which has not previously received much attention.

The conclusion which we draw from these experiments is that in the elasmobranch fishes, such as the skate, the gastric secretion is regulated in a different manner from that of other vertebrates. Thus in the higher mammalian forms (such as the cat, the dog, or man) gastric secretion is regulated chiefly by the parasympathetic, and to a lesser degree by the sympathetic nervous system. The existence in these mammals of a humoral mechanism is also recognized. In amphibians, *e.g.*, the frog, it is the sympathetic nervous system and not the vagus which chiefly supplies the gastric mucosa with secretory fibres (Friedman 1934). Practically nothing is known about the humoral regulation of the gastric secretion in the frog.

In the skate, the gastric glands are in a continuous, though comparatively insignificant, state of (secretory) activity. Very strong evidence was obtained in this investigation in support of the view that this spontaneous secretory activity does not depend on the direct influence of either the parasympathetic or the sympathetic nervous system, but that it is greatly influenced by changes in the abdominal circulation. This condition is all the more remarkable considering that the motor innervation of the stomach in elasmobranchs is well developed (Babkin, Friedman and MacKay-Sawyer 1935).

Destruction of the spinal cord leads to a "paralytic" gastric secretion unusually large in volume. It is highly probable that this secretion is of vascular origin and depends on the lowered tonus and possibly on the resultant increase in the permeability of the blood vessels supplying the gastric mucosa (Chaisson and Friedman 1935). When the secretion lasts long enough in a starving "paralytic" animal, it is found that the blood becomes gradually depleted of

some of its electrolytes, as may be judged from the diminution of its osmotic pressure. Further investigation is required in order to determine what components of the blood are lost during "paralytic" secretion and are not replaced.

The phenomenon of "paralytic" secretion of gastric juice in the elasmobranchs is reminiscent of the effect which unilateral section of the splanchnic nerve produces on kidney secretion in warm-blooded animals. In both cases changes in the circulation within the organ greatly increase the activity of the secretory epithelium of that organ.

SUMMARY

1. A fasting skate continuously secretes a small volume of gastric juice of high acidity.

2. This spontaneous secretion is not influenced either by section of both vagi or by administration of atropine. Stimulation of the anterior splanchnic nerves or administration of adrenaline inhibits the secretion. Administration of histamine has apparently no effect on the secretion.

3. Destruction of the spinal cord, and hence elimination of the influence of the central part of the sympathetic nervous system, provokes a "paralytic" gastric secretion. This secretion commences 24 hours to three or four days after the operation, and may last for many days (longest term of observation, 16 days).

4. The volume of the "paralytic" secretion varies from day to day. It is acid, having an average pH lying between 2.0 and 3.5. The freezing point of this secretion rises gradually towards zero, though the Cl concentration remains more or less constant. Adrenaline stops the paralytic secretion for several hours.

5. The theory is advanced that the "paralytic" secretion is due to some vascular changes in the abdominal viscera, arising as a result of the disconnection of the peripheral parts of the sympathetic nervous system from its central apparatus.

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The Function of the Claspers and Clasper-Glands in the Skate

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ABSTRACT

The clasper is erected by powerful adductor muscles as well as by vascular dilatation and is used as an organ of intromission. The gland secretes simultaneously from all its papillae a fluid which washes sperm down the clasper-tube into the female's cloaca. A centre for clasper erection exists in the cord between spinal nerves 48 to 50. In a spinal male tapping on the anal region causes a reflex erection of the claspers. Adrenaline apparently lowers the stimulus threshold for clasper erection.

INTRODUCTION

During the course of work with Prof. B. P. Babkin on the influence of the autonomic nervous system on the gastric functions of the skate we had occasion to destroy the spinal cord by passing a long probe from below the medulla down the vertebral canal. We noticed that whenever the probe reached a certain level in the canal of male skates there would occur strong, jerky movements or erections of the anal appendages or so-called "claspers", and that the distal ends of these claspers would open widely. The picture was very striking in character and since the significance of the movements was obscure we undertook certain experiments on these organs.

The animals used were chiefly huge specimens (125 cm. length and 25 kg. weight) of the barndoor skate, *Raja stabuliforis*. By employing these animals we had a distinct advantage in anatomy over other workers, nearly all of whom used much smaller species of elasmobranchs. In addition we used two smaller species of skate, *R. erinacea* and *R. diaphanes*, which usually measured about 55 cm.

ANATOMICAL DATA

The following anatomical relations were found to exist in *R. stabuliforis* and were compared with descriptions given for other elasmobranchs by previous workers, chiefly Leigh-Sharpe (1920, 1921, 1922). The three species of skates we examined differed only in minor details and the relations were found to be essentially the same as in the other species described by Leigh-Sharpe.

The claspers and clasper-glands are present in male elasmobranchs only. The cartilaginous basipterygium of the pelvic fin is prolonged to a stout skeletal rod and supports the medial portion of the fin. This part of the fin is sharply divided from the rest and forms the clasper. The clasper is not a solid mass but is rather a part of the fin rolled up to form a tube whose edges are not fused, but overlap. Following the nomenclature given by Leigh-Sharpe (1920), the anterior proximal opening of this tube may be designated as the apopyle and the posterior distal exit from the tube as the hypopyle. In the skate the apopyle is several centimetres posterior to the anus whereas in the dogfish and shark it is close to it.

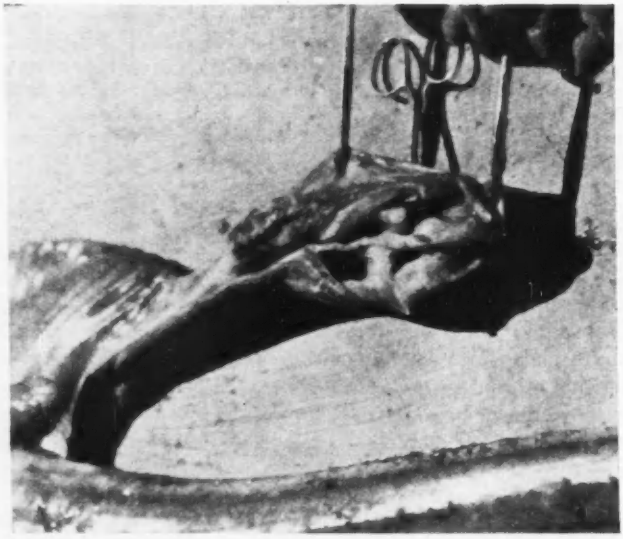

FIGURE 1. *Raja stabuliforis*. Dorsal view, showing the clasper in the open state. The groove along the length of the clasper represents the fold enclosing the clasper-tube; the distal opening of the clasper-tube can be plainly seen.

On the abdominal side, a short distance anterior to the base of the clasper, there is a sac situated just under the skin. According to Leigh-Sharpe (1920) in dogfish and sharks this sac is empty and is called the syphon. In the skate, however, this sac is nearly completely filled by a gland attached to the dorsal wall of the syphon sac. The clasper-gland is a bilobed structure with a longitudinal groove running along the centre of its ventral surface; within the groove there are several rows of papillae, and any secretion from the gland is expelled by these papillae into the syphon sac. The syphon sac has no communication with the coelome, but has a narrow duct leading from its posterior end to open

at some point in the clasper-tube. This duct is, therefore, the ultimate path taken by the secretion after it leaves the gland.

According to Leigh-Sharpe (1920), both the syphon sac and the superficial layer of the gland are very muscular. Under a suitable stimulus the gland contracts segmentally and we observed a semi-viscous, milky-white fluid to gush out from all of the papillae, although Leigh-Sharpe (1922) observed fluid to come out from only certain papillae at a time. The contraction of the muscular syphon now sends this secretion with a tremendous speed into the syphon duct and so down into the clasper-tube.

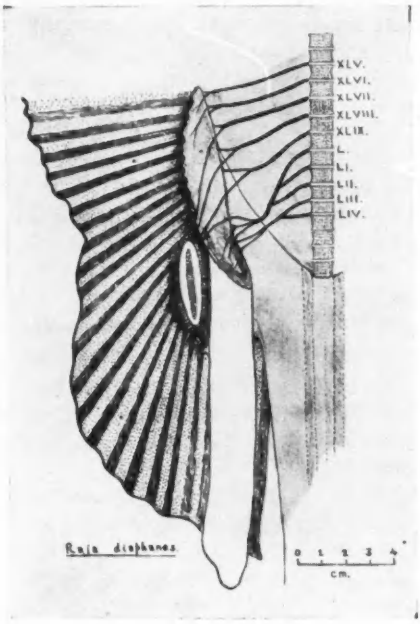

FIGURE 2. *Raja diaphanes.* Ventral aspect, showing the nerve supply to the clasper and the clasper-gland. The syphon sac is open to expose the gland. Note the bi-lobed appearance of the gland with the rows of papillae in its longitudinal groove.

The posterior end of the clasper carries within the hypopyle a cartilaginous structure, the rhipidion. The apparent purpose of this organ is to cause any liquid passing down the clasper-tube to spread out into a fan-shaped stream. (See figure 1).

EXPERIMENTAL RESULTS

Dissection of the male skate showed us that the clasper is innervated by branches of five spinal nerves, the 50th to 54th inclusive; and possibly also by

a sixth, namely, the 55th. The clasper-gland is usually innervated by three nerves, spinal nerves 47, 48, and 49; the exact number, however, is uncertain since it seems to vary in different fishes. (See figure 2).

In the skate the spinal roots, both ventral and dorsal, run within the vertebral canal for a distance of about two vertebrae before they pass through the vertebral column to form the mixed nerve; and in the large *R. stabuliforis* the spinal roots may be nearly three centimetres long.

Faradic stimulation of the intact dorsal root (ventral root left intact) gave only a slight clasper response; stimulation of the peripheral end of the cut dorsal root was without effect. Either the whole ventral root or the peripheral end when stimulated resulted in movement of various parts of the body. Spinal (ventral) roots 50 to 54 caused erection of the clasper by means of muscles, and the opening of its distal end or lips. Spinal nerve 55 occasionally resulted in just the opening of the clasper lips. When the clasper is made to open passively, there is seen on the rhipidion little to indicate a network of blood vessels; but when stimulation causes the opening of the clasper, a large fine meshwork of blood-vessels is seen, all fully suffused with blood.

Stimulation of the ventral roots of spinal nerves 47, 48, and 49 resulted in secretion from the gland. This effect was best seen when the 49th was stimulated, and could often be observed when the 50th, which innervates chiefly the clasper, was stimulated.

Stimulation of the nerves (or their ventral roots), which supply the clasper-gland and the syphon wall, resulted in a striking response. There would be an instantaneous contraction of the syphon wall so that the volume of the syphon sac was reduced to about half its former size. If the gland was exposed and the nerves stimulated, there was an immediate segmented contraction of the whole gland, the surface became entirely suffused with blood, and all the papillae gushed a milky-white semi-viscous fluid.

The secretion from the gland coagulated immediately it came in contact with sea-water or blood. On one occasion about 5 cc. of the secretion was collected in a test-tube, but within twenty minutes it solidified and could only be reached by breaking the test-tube. According to Leigh-Sharpe (1922) the secretion from the skate (*R. clavata*) is albuminous in nature; he claims that it comes only from a few papillae at a time in the form of long fine strings. We observed the secretion to be a semi-viscous fluid when it first came from the papillae and not in the form of a stringy mass; furthermore, in our experiments the secretion certainly came from all the papillae at the same time.

A striking point in our observations is that the surface of the gland and the small network of blood vessels on the rhipidion become immediately suffused with blood when the nerves are stimulated, and almost as instantaneously lose their blood supply when the stimulus is removed. It is possible that this signifies the presence in the 50th to 54th ventral roots of vaso-dilator nerve fibres. Although in the species dealt with here the vascular network is small and its gorging with blood cannot by itself be responsible for the clasper erection, in some species the mechanism of erection is similar to that in the mammalian

penis. According to Leigh-Sharpe (1920, 1921) the clasper of *Raja circularis* and *Galeus vulgaris* has a minimum of cartilaginous but an excess of erectile tissue; in the first-named species the claspers were found after copulation to be swollen by blood to several times their normal size. In the species we examined, however, erection is nearly wholly dependent on muscular adduction rather than blood suffusion.

Stimulation of the spinal cord in the region between spinal nerves 48 and 54 resulted in erection of the clasper, contraction of the gland, and secretion. If spinal roots 50 to 53 were cut so that only the 54th was connected with the clasper, stimulation of the cord in the region of the origin of the 48th to 50th nerves would produce an instantaneous erection of the clasper. Stimulation of the cord above the 48th or below the 50th was without effect. This would indicate that there exists within the spinal cord in the region of the 48th to 50th nerves a centre for clasper erection.

Administration of adrenaline gave interesting results. Three male skates (*R. diaphanes*) were given subcutaneous injections of 22 cc. of 1:10,000 adrenaline over a period of 22 hours. No erection or other movements of the claspers were observed throughout this period. At the end of this time, the spinal cord of each was cut below the medulla oblongata. There was an immediate erection and opening of the claspers in all three animals, and they stayed erect and open for more than 45 minutes. Cutting the spinal cord of a normal animal may at times produce a few jerky movements of the claspers, but they do not remain erect for more than about a minute. In a number of animals the spinal cord was cut first and then adrenaline injected, but no erection ever occurred; it must be added, however, that in these instances the amount of adrenaline was not large (1 to 2 cc. of 1:10,000). The real cause of the phenomenon is not known; possibly adrenaline raises the excitability of either the clasper muscles or the centres in the spinal cord. After removal of the inhibitory influences of the brain by section of the spinal cord, the normally ineffective reflex stimuli become capable of producing the erection. Or else, in sectioning the cord, nerve fibres going to the claspers are stimulated to produce the erection. This phenomenon is strikingly similar to the reported erection of the penis which occurs in the human male when in a period of intense excitement (during which he is presumably secreting large amounts of adrenine) his spinal cord is severely injured in the cervical region, as in criminals when hung.

In her study on the spinal reflexes of the skate, Craw (1927) makes no mention of clasper reflexes. We observed that tapping the region around the anus in a spinal skate, and less often in a normal animal, produces a reflex erection and sometimes also the opening of the clasper lips, but apparently no secretion from the clasper-gland. It is probable that this is a mode of erecting the claspers in the skate before coitus since the anal region of the male is more or less constantly rubbed by the tail or abdominal side of the female.

DISCUSSION

For long the function of the claspers in elasmobranchs was not clear. Aristotle stated that the clasper was characteristic of the male cartilaginous fishes only, and observed that during copulation the animals "hang together after the fashion of dogs, the long-tailed ones mounting the others, unless the latter have a thick tail preventing this, when they come together belly to belly." That the clasper was an organ of intromission, like the penis of a mammal, was held by Willoughby, Ray, Artedi and Broussonet (*vide* Davy 1839), but this idea soon gave way to the opinion that the claspers were used by the male as holders, analogous to hands (or rather feet) for seizing and holding the female. This view was sponsored by Rondellet and by Block (Davy 1839)—by the latter on anatomical grounds—and it is because of their work that these anal appendages have come to be known as "claspers".

In 1839, John Davy once again revived the view that the clasper is an organ of intromission. He did this, however, with great caution, writing, "In venturing to bring forward this conjecture, I beg to be understood that I attach no kind of importance to it." He found in the gland of *Raja batis* a "cream-like secretion. . . . It was neither acid nor alkaline; it was slightly viscid; applied to the tongue . . . there was an after-(sensation) approaching to acid." He did not find any spermatozoa in the gland, and concluded that the secretion was for the purpose of lubrication.

Louis Agassiz (1858) apparently unaware of Davy's work, also held that the clasper was an organ of intromission. To assign a function to the syphon, he unfortunately formulated the erroneous opinion, later widely copied, that the syphon was a reservoir for spermatozoa. According to Agassiz (1871) one or both claspers were introduced into the cloaca of the female. He regarded the clasper as homologous to the mammalian penis and proposed to study the connection between the movements of the claspers and the pelvic fins, and the movements of the mammalian penis and muscles of the hind legs. In these views, Agassiz was closely supported by Garman (1875, 1877). On the rhipidion of the clasper there are in some species of skates sharp hooks, the purpose of which is apparently to puncture the membrane or hymen closing the oviduct of the virgin female. (A diagram of the hymen separating the oviduct from the cloaca will be found in Daniel (1928, p. 309)). Garman (1875) pointed out that in the adult male skate there are near the outer borders of the pectoral fins two or more rows of long pointed hooks; these are capable of erection and retraction. It is with them that the male skate is enabled to hold and turn the female so that their ventral surfaces should be brought together.

When the male is holding the female, his pectoral fins are folded under him so that the peripheral row of retractile hooks on the fin are now ventral in position with respect to the rest of the body. These hooks are sunk into the ventral surface of the female and thus keep the abdomens of both animals in contact with each other. The pressure or touch on the anal region of the male by the female may now serve as a stimulus for the erection and insertion of the claspers into the cloaca of the female. According to Garman (1877) the claspers are

brought upward and inward by bending at the base, making the upper part come in contact with the anus.

Agassiz (1871) held that both claspers are introduced at the same time into the female cloacal aperture and that their extremities diverge into the two oviducts. On anatomical considerations it would seem to us that this would be possible only if the claspers were crossed when introduced, so that the right clasper entered the right oviduct and the left clasper the left oviduct. In many instances we observed that when both claspers were erected they would be crossed in the manner of two swords to form the letter X. According to Bolau (1881), who observed that coition in *Scyllium* lasted 20 minutes, only one clasper is introduced at a time. Leigh-Sharpe (1922) also states that only one clasper is introduced at a time. In view of the fact that all adult female skates we examined had fertilized eggs in both oviducts, it would seem that both claspers are introduced into the female body at once or else that one clasper is introduced alternately into each oviduct.

It is from the work of Leigh-Sharpe (1920) that the use of the syphon and the clasper-gland becomes clear. During the mating season sperm is constantly dribbling out of the cloaca of the male and some of it finds a way into the anterior opening of the clasper tube, or apopyle. The entrance of the sperm into the apopyle may be perhaps made more certain if, as Garman (1877) stated, the upper part of the clasper is in contact with the anus when it is erected. In this connection we noted that the apopyle is widened when the clasper is erected. Contraction of the syphon will cause a flow of fluid through the syphon duct and into the clasper tube, and this stream of fluid will thus carry the sperm along to the distal end of the clasper. In sharks and dogfish the syphon contains seawater; in skates the syphon contains a gland which secretes a special fluid for this purpose. In function therefore the clasper-gland is analagous to the prostate gland of the mammal.

SUMMARY

The "clasper" and "clasper-gland" in the male skate show a striking similarity of function to the mammalian penis and prostate gland respectively. Efferent nerve fibres to these sex organs course through the ventral spinal roots (nerves 47 to 54) and not through the dorsal spinal roots. There exists within the spinal cord in the region giving off spinal nerves 48 to 50 a centre for clasper erection. Vasodilator fibres are probably present within the ventral roots of spinal nerves 50 to 54. Adrenaline raises the excitability of either the clasper muscles or the centres in the spinal cord. A reflex erection of the claspers can be obtained by tapping the anal region of the spinal skate.

The secretion, which comes from all the papillae of the clasper-gland, is a milky-white semi-viscous fluid, which coagulates rapidly on contact with seawater or blood.

The use of these organs is discussed.

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interest in the work and for his numerous helpful suggestions. He wishes also to thank the Biological Board of Canada and the Director of the Station for the facilities afforded and Mr. J. A. Stevenson for help in the taking of the photograph shown in figure 1.

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Lobster Tagging in the Gulf of St. Lawrence

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ABSTRACT

An individual lobster may occasionally move several kilometres in one day, yet the resultant of all the movements of a group of lobsters during the year is an average removal of only about 8 kilometres from their point of liberation. An occasional lobster, however, may have wandered 30 to 40 kilometres away during this time. The lobsters scatter equally in both directions along shore. Females apparently wander further than males. The intensity of fishing is very high in the areas examined, probably about 40 per cent of the larger lobsters being caught during a two month fishing season.

INTRODUCTION

The chief practical object to be attained by lobster tagging is the resultant of the movements of the lobster during a whole year's migrating. Do the lobsters in a certain area move enough as a result of their offshore, onshore and alongshore migrations to populate another area of coast several or many kilometres away? Previous tagging has failed to answer this question. In the case of the tagging of lobsters by the U.S. Bureau of Fisheries (Bumpus 1901) and by the Rhode Island commission (Mead 1904, 1905; Barnes 1906, 1907) tagging was confined to female lobsters which had just hatched their eggs or from which the well developed eggs had been removed. Since female lobsters usually moult soon after their eggs have hatched, with a resulting loss of the tags, little information could be obtained as the lobsters were merely free for one to eighty-nine days before being recaptured.

Dannevig (1927), from lobster marking in Norway, says that "over half were recaptured in the same locality after two years and only one was caught two nautical miles from its point of release." Dannevig marked the lobsters by cutting notches in the margins of the uropods. These marked lobsters could still be distinguished after several years. The method, however, suffers the disadvantage that lobsters captured in the immediate area under observation would be reported, but occasional recaptures in areas further away would generally pass unnoticed, or if noticed would be taken for lobsters mutilated by their fellows.

Since there is no absolutely successful method of finding the migration of the average lobster over long periods, in our experiments we have used new shell lobsters which had moulted only a few days or weeks previously, the lobsters

being tagged with a numbered metal tag through the telson. These new shell lobsters, especially the larger, would remain about a year before moulting again. The tags used are very conspicuous and the whole area for several hundred kilometres or more on either side of the tagging spot was circularised—a printed notice being placed in each lobster cannery before the lobster fishing season opened, announcing that lobsters were being tagged, the method of tagging, and that 25 cents would be paid for the return of each tag to the Biological Station at St. Andrews. The collecting of the tags was usually undertaken by the fishery officers, who took an active interest in the tagging operations. Under these conditions tagged lobsters caught at considerable distances from the point of liberation would have a good chance of being reported.

The lobster tagging in western Northumberland strait in 1930 was carried out by Professor A. F. Chaisson of St. Francis Xavier University and by the author; in Malpeque bay in 1931 by Mr. R. V. V. Nicholls of McGill University under the direction of the author. The remainder of the tagging was performed by the author himself.

MIGRATION AND WANDERING

Between July 2 and August 10, 1931, a total of 918 lobsters were tagged and liberated in various parts of the Magdalen islands area, and of these 152 were recaptured between May 11 and July 19, 1932. The 9 to 12 month period intervening between liberation and recapture would include the fall offshore and spring onshore migrations, which are supposed to occur in the lobster, as well as allowing sufficient time for alongshore migrations to take place.

Figure 1 shows the resultant of the total movements during this 9 to 12 month period of lobsters liberated at various points off Grindstone island, Magdalen islands. Many of the tagged lobsters were caught at the point where they were liberated 9 to 12 months previously, while approximately equal numbers of lobsters were caught on either side of the liberation point (figure 1, B and C). As shown in figure 1, A and B, and to some extent in C, lobsters which moved toward the north travelled considerably further than those moving south. South of Grindstone island the bottom of Pleasant bay is sandy, while for a considerable distance north from the points of liberation the bottom is more or less rocky. In view of the well known preference of the lobster for rocky bottom there is no need to assume that most of the lobsters were migrating to the north, but rather that a gradual wandering away from the liberation point took place, and that the sandy bottom to some extent checked the wanderings at the southern end of Grindstone island.

Figure 2 indicates the recaptures of tagged lobsters liberated mostly in the lagoons of the Magdalen islands and at liberty for the above 9 to 12 month period. Fishing is not permitted in these lagoons since they are regarded as lobster sanctuaries. Special fishing in House harbour lagoon in July and August 1931 revealed large quantities of lobsters, and showed the moulting period in this lagoon to be three weeks earlier than in the neighbouring parts of Pleasant bay outside the lagoon. It was thus thought that the lagoon lobsters might possibly

be a local population. The recaptures, however, shown in figure 2 prove that lobsters migrate out of all these lagoons and, as shown especially in figure 2B, spread equally north and south along the shore. In view of the early moulting it is probable that the lobsters move into the lagoons very early in spring and probably in the main move out again in the fall.

Figure 3, A and B, indicate the points of recapture of tagged lobsters liberated at the mouth of Bideford river and at Bunbury island reef, Malpeque bay, from July 24 to August 14, 1931, and recaptured between May 1 and June 30, 1932. The effects of wandering rather than a definite migration along shore are again evident, although in figure 3A there is a greater movement towards the east

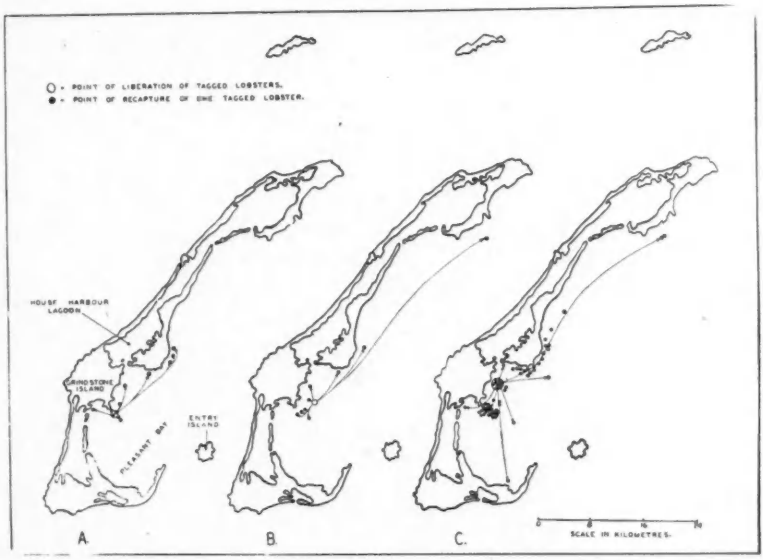

FIGURE 1. Movements of tagged lobsters liberated July 2 to August 10, 1931; A, off Red cape; B, off Gaudet's point; C, at Meule rock, Magdalen islands. Recaptured between May 11 and July 19, 1932.

than to the west, but this is to be expected, since a fall offshore migration from Bideford river to deeper water would take the lobsters towards the middle of Malpeque bay, from whence the spring onshore migration would distribute them to many different parts of the bay.

RESULTANT OF YEARLY MOVEMENTS OF A LOBSTER POPULATION

Figure 4 is a diagram showing the resultant distances travelled in $8\frac{1}{2}$ to 12 months by the lobsters liberated in the Magdalen islands area and in Malpeque bay and represented in figures 1, 2 and 3. The diagram was composed under the assumption that if bottom conditions are similar the lobsters wander equally

in both directions along shore. A lobster liberated at Bideford river travelled furthest—43 kilometres. Six other lobsters were recaptured 32 to 35 kilometres away from the point of liberation. Only 19 out of 222 lobsters were more than 16 kilometres from their liberation point after 8½ to 12 months of wandering. These 222 lobsters were on the average recaptured 8 kilometres away from their point of liberation (table I). They were at liberty to move during the periods of the year when migration is most to be expected, namely spring and fall, and the only part of the year not properly covered by the experiment—late June and early July—is the period when the lobsters in these areas are moulting and are very sluggish. Thus the resultant of all the movements of a lobster during

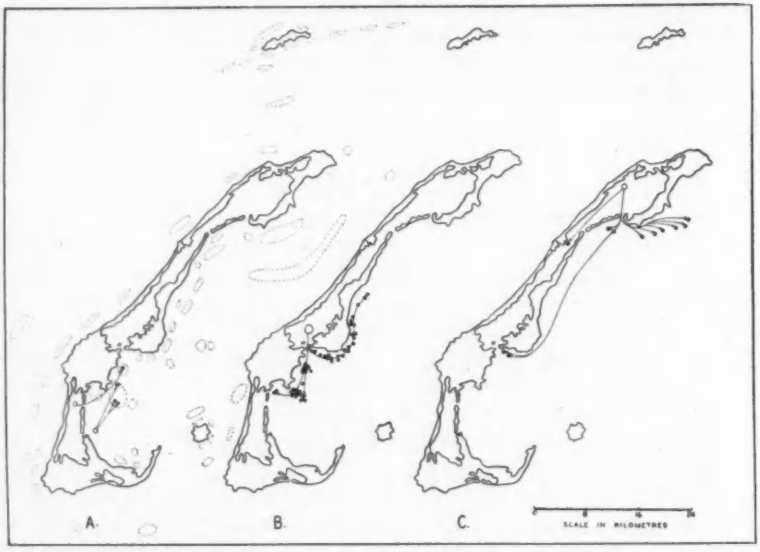

FIGURE 2. Movements of tagged lobsters liberated July 2 to August 10, 1931: A, in or near Basque harbour lagoon; B, in House harbour lagoon; C, in Grand Entry lagoon, Magdalen islands. Recaptured between May 11 and July 19, 1932. Dotted areas in A are the principal lobster fishing grounds of the Magdalen islands according to information received from Mr. William Arsenault, Fisheries Inspector, Grindstone.

one year is a removal of its place of residence on the average about 8 kilometres in one direction or another along the shore.

Although lobster fishing is carried on in many areas around Entry island and on the western side of the Magdalen islands group, none of the lobsters tagged on the eastern side was caught at Entry island nor on the western side; neither were any lobsters tagged in the Magdalen islands area caught in any other section of the gulf.

In western Northumberland strait, where 831 lobsters were tagged in late August and early September of 1930 and 1931, and only 224 were recaptured.

none of the survivors was caught during the following May and June open season in the areas on either side, although the region with a May and June open season began only about 50 kilometres west of the Pointe du Chêne liberation area and about 50 kilometres east of the Summerside point of liberation. These new shelled lobsters tagged in late August and September would not moult before the latter part of June or early July of the succeeding year.

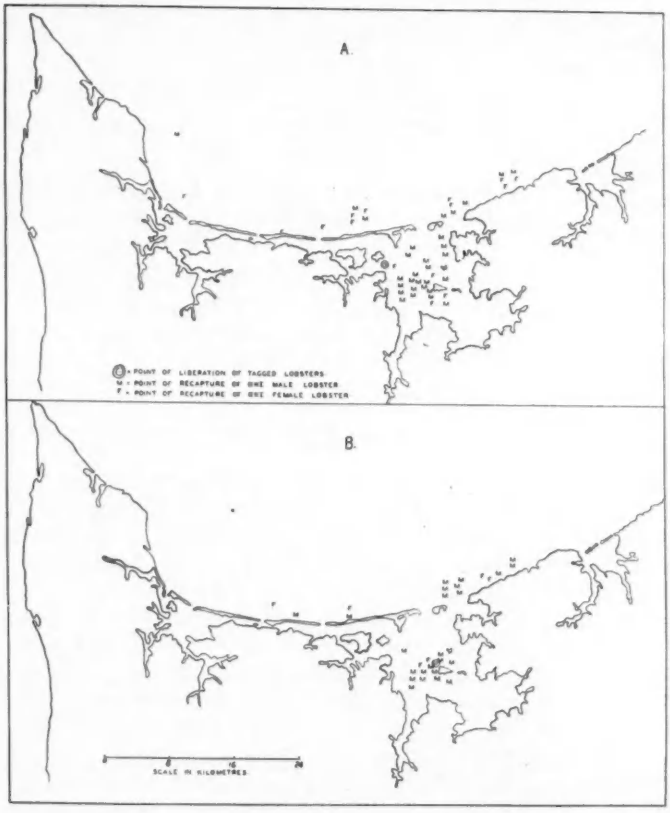
A.
O - POINT OF LIBERATION OF TAGGED LOBSTERS.
M - POINT OF RECAPTURE OF ONE MALE LOBSTER
F - POINT OF RECAPTURE OF ONE FEMALE LOBSTER
B.
SCALE IN KILOMETRES

FIGURE 3. Movements of tagged lobsters liberated July 24 to August 14, 1931: A, at the mouth of Bideford river; B, at Bunbury island reef, Malpeque bay. Recaptured between May 1 and June 30, 1932.

The fact that no recaptures were reported in the above circumstances adds strength to the argument that lobsters do not undergo extensive migrations from one area to another along the coast, the various populations retaining their essentially local character for many months and gradually mixing with the surrounding population by directionless wandering.

TABLE I. Wanderings of lobsters liberated in the Magdalen island area July 2 to August 10, 1931, and recaptured May 11 to July 19, 1932; and of lobsters liberated in Malpeque bay, P.E.I., July 24 to August 14, 1931, and recaptured May 1 to June 30, 1932.

Liberation point	Number recaptured	Total distance from point of liberation when recaptured (km.)	Average distance from point of liberation when recaptured (km.)
Magdalen islands			
Off Red cape	12	54.9	4.6
Off Gaudet's point	9	62.4	6.9
Meule rock	63	322.6	5.1
In or near Basque harbour lagoon	4	28.3	7.1
House harbour lagoon	50	448.8	9.0
Grand Entry lagoon	10	164.0	16.4
Malpeque bay			
Mouth of Bideford river	44	460.0	10.5
Bunbury island reef	30	245.6	8.2
Total	222	1786.6	8.0

SPEED OF INDIVIDUAL LOBSTERS

Although the resultant of the yearly travels of the average lobster is merely a removal to fishing grounds a few kilometres away, lobsters possess the power of travelling remarkably quickly.

In the tagging experiments carried on by Bumpus in 1898 at Woods Hole one lobster travelled 19 kilometres in 3 days, another 24 kilometres in 6 days and still another 24 kilometres in 7 days. These represented the exceptionally fast travellers of 76 lobsters which were free for an average of 24 days, travelling on the average 7.7. kilometres during this time.

Table II shows the average wanderings per day of the fastest travellers in

TABLE II. Rapidity of movement of lobsters liberated in western Northumberland strait in late August and early September 1930 and 1931

Length (cm.)	Sex	Number of days free	Distance from point of liberation when recaptured (km.)	Average distance travelled per day (km.)
22	F	1	6	6
20	M	2	6	3
19	M	3	9	3
23	M	3	9	3
22	M	6	6	1
21	M	8	17	2.1
19	F	9	24	2.7
22	F	21	27	1.3
22	M	21	17	0.8
22	M	32	24	0.8

a group of 766 lobsters tagged during August and September, 1930—31 at Pointe du Chêne, N.B., of which 209 were recaptured within 1 to 45 days after liberation. The fastest traveller moved 6 kilometres in one day, while several appar-

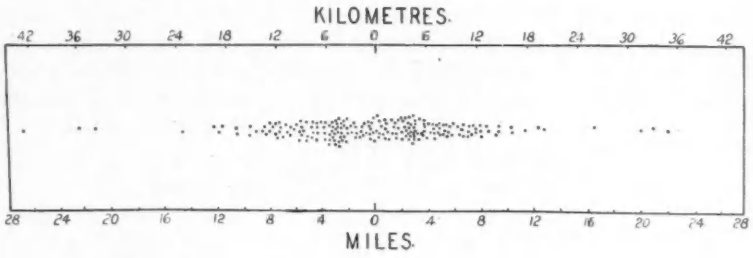

FIGURE 4. Combined diagram of the alongshore wanderings of the lobsters shown in figures 1, 2 and 3. Zero represents the point of liberation of the lobsters.

ently continued to move at the rate of 3 kilometres a day for several days. Another moved 24 kilometres in 9 days. The longer the lobster was free the smaller in general was the distance travelled per day.

FEMALES TRAVEL FURTHER THAN MALES

Figure 3 shows the points of recapture of male and female lobsters liberated at the mouth of Bideford river, Malpeque bay, and on Bunbury island reef in July and August 1931. Of 336 males liberated in Malpeque bay in 1931, 54 were recaptured in 1932. Of these 65 per cent were recaptured inside and 35 per cent outside Malpeque bay. Of 124 females liberated at the same points in Malpeque bay in 1931, 20 were recaptured in 1932. Of these only 30 per cent were recaptured within Malpeque bay while 70 per cent were recaptured outside the bay. The males were recaptured on the average 8.0 kilometres away from the point of liberation while the females were found on the average 13.6 kilometres away from the liberation point. Nearly all of these recaptured males and females were sexually mature.

On the data available at present it is difficult to interpret exactly this remarkable difference in behaviour between the two sexes. Two possibilities present themselves. (1) The sexually mature female lobsters may be more inclined than the males on the approach of winter conditions to seek deeper water than is to be found in Malpeque bay. (2) The females which leave the bay in the fall may remain longer than the males in the offshore water during the spring and early summer before again moving into the bay. Herrick (1911) says

"The general movement of lobsters toward the shore in the spring is modified by reason of females with old eggs finding it advantageous to remain on rocky ledges until the young are hatched, while the males press onward to shallower water. After hatching is over, the females make their appearance in larger numbers in the sound towards the last of June or 1st of July."

It is probable that both of the two possibilities presented above have a share in the wider distribution of females than of males liberated in such an area as Malpeque bay.

MOULTING

As shown in table III, of the 1378 lobsters tagged in the Magdalen islands and in Malpeque bay in July and August 1931, very few of the smaller sizes were recaptured from May to July, 1932. Since all these lobsters were new shelled

TABLE III. Lobsters tagged and liberated at the Magdalen islands and in Malpeque bay July 2 to August 14, 1931, and recaptured May 1 to July 19, 1932.

Male				Female		
Percentage recaptured	Number recaptured	Number tagged	Length cm.	Number tagged	Number recaptured	Percentage recaptured
4.3	1	23	15-19	26	2	7.7
9.1	23	253	20-23	122	10	8.2
17.4	93	533	24-27	100	21	21.0
25.3	67	265	28-31	12	4	33.3
11.4	5	44	32-36			
16.9	189	1118	Total	260	37	14.2

and had moulted only a few days or weeks before being tagged, it is indicated that a great number of these smaller lobsters of commercial size moulted again between July and August 1931 and May and July 1932. Since the first moulting of the year begins only during the last two weeks of the legal fishing season in both the above areas, the second moulting referred to above would have occurred mostly in the fall of 1931. Thus in these areas two moultings per year occur among the smaller lobsters, say 16 to 22 cm. in length, as has already been found by the author to be the case at Pointe du Chêne, N.B., by special fishing.

The greatest intensity of fishing in these areas falls upon lobsters from 16 to 18 cm. and upwards, so that failure of the traps to hold the small lobsters would not act to produce the discrepancies shown in table III between the recaptures of small and large lobsters.

During the fishing season May to July 1933 absolutely no recaptures were reported from the lobsters tagged in 1931. It is thus evident that even the largest lobsters tagged in 1931 moulted during the year 1932, so that in general even among the largest male lobsters normally occurring in the Malpeque bay and eastern Magdalen island catches moulting occurs once per year. The above statement applies with more force to the large males than to the large females, for as shown in table III, very few large females were tagged, and although no recaptures were reported in the second year, it is undoubtedly true that many mature females of the sizes tagged pass several years without moulting.

INTENSITY OF FISHING

Bumpus (1901) reports that of 479 female lobsters liberated at Woods Hole during June and July 1898, 16 per cent were recaptured within 89 days of liberation. Of 497 female lobsters liberated at Wickford R.I., in 1902 and 1903, 9 per cent were recaptured within 75 days of liberation (Mead 1904).

491 male and 275 female new shell lobsters 18 to 24 cm. in length were tagged and liberated at Pointe du Chêne, N.B., from August 23 to September 2, 1930 and 1931. As shown by measurements in this area the greatest intensity of fishing at Pointe du Chêne falls on lobsters of 18 to 19 cm. and upward. The sizes tagged, 18 to 24 cm., were therefore fully susceptible to capture. The fishing season in the western Northumberland strait area is from August 16 to October 15. Since the lobsters were tagged and liberated from August 23 to 25 in 1930, and on September 2 in 1931, and recaptured in the same year, only 43 to 52 days were available for recapturing the tagged lobsters, yet in this short time 28.7 per cent of the males were recaptured and 24.7 per cent of the females. Some of the lobsters undoubtedly lost their tags. Other tags were not reported and a very large proportion of the lobsters in this area are caught during the first two weeks of the fishing season. No tagged lobsters were at liberty during the first week of the open season in 1930 nor during the first two weeks in 1931. Thus it is probable that in the neighbourhood of 40 per cent of the lobster population above 18 cm. in length is caught in the above area during each lobster season. Females above 18 cm. are slightly less likely to be caught than males.

Of 1118 male and 260 female lobsters 15 to 36 cm. in length, tagged and liberated near the Magdalen islands and in Malpeque bay in 1931, 16.9 per cent of the males and 14.2 per cent of the females were recaptured in 1932 (table III). The percentage recaptured is low, since many of the smaller lobsters have presumably moulted and a considerable number of the tags have probably been lost during the 8½ to 12 months at liberty. At sizes larger than 23 cm., which would presumably be little affected by a second moult in this period, 20 per cent of the tagged lobsters were recaptured. Again allowing for factors such as loss of tags and failure of fishermen to report tags, a large percentage of the lobster population is captured in the 2½ months fishing season in these areas. The smaller percentage of females than males recaptured is largely due to the fact that a relatively greater number of smaller females than males were tagged, and at these smaller sizes there were few recaptures.

SUMMARY

The following conclusions were derived from the recapture of 450 lobsters out of 2209 tagged in the southern part of the gulf of St. Lawrence during 1930 and 1931.

(1) Large quantities of lobsters migrate out of the lagoons of the Magdalen islands, probably in the autumn.

(2) The alongshore movements of the lobster are the result of directionless

wandering, the lobsters moving approximately equally in both directions if bottom conditions are similar.

(3) Of 222 recaptured lobsters which had been free from 8½ to 12 months, the best traveller was recaptured only 43 kilometres away from the point of liberation, only 8.6 per cent had travelled further than 16 kilometres, and the lobsters as a group were recaptured on the average 8 kilometres away from their liberation point.

(4) With lobsters at liberty for shorter periods one lobster moved 6 kilometres in one day, while several apparently moved at the rate of 3 kilometres a day for 2 or 3 days.

(5) Female lobsters in such an area as Malpeque bay either have a greater tendency to leave the bay in the autumn, or they remain longer than the males in deep water during the spring. Both may occur.

(6) A large percentage of the smaller lobsters, about 16 to 22 cm. in length, in Malpeque bay and in the lagoons and Pleasant bay, Magdalen islands, moult twice during the year, while the males of sizes as large as 30 cm. moult once per year.

(7) It is probable that as much as 40 per cent of the lobster population over 18 cm. in length is caught during several months' fishing in many of the southern gulf of St. Lawrence areas.

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